Vertebrate Palaeoichnology of the Lower Cretaceous (lower Albian) Gates Formation of Alberta

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ABSTRACT

Western Canada has few significant skeletal remains of terrestrial vertebrates from the Lower Cretaceous. The only substantial record of Early Cretaceous terrestrial vertebrates comes from footprints. The Grande Cache Member of the Gates Formation, on the coal lease property of Smoky River Coal Limited in western Alberta, exhibits abundant footprint traces of vertebrates from the Lower Cretaceous (Albian). The vertebrate ichnofauna described herein (Smoky River ichnofauna) includes footprints of dinosaurs (theropods, ?ornithopods and thyreophorans), birds and mammals. The Smoky River ichnofauna consists of eight ichnospecies assigned to seven ichnogenera. Two new ichnospecies, *Aquatilavipes* ichnosp. nov., and ?*Tricorynopus* ichnosp. nov., are described and the definitions of the ichnotaxa *Irenesauripus mclearni*, *Columbosauripus ungulatus*, *Gypsichnites pacensis*, *Irenichnites gracilis*, *Tetrapodosaurus borealis*, *Aquatilavipes* and *Fuscinapeda* are emended.

Previous perceptions of the Lower Cretaceous terrestrial vertebrates from Canada came from the studies of the ornithopod-theropod dominated Peace River Ichnofauna from British Columbia. Large-scale tracksites from the Gates Formation within the Smoky River Coal Mine dominated by the footprints of ankylosaurs has shed new light on the composition of Lower Cretaceous vertebrate ichnofaunas.

The distribution of ichnotaxa at these tracksites may indicate habitat preference for some of the track-makers, possibly controlled by the energy of the depositional environments and presence of vegetation.

ACKNOWLEDGEMENTS

I would like to thank my two research supervisors, Dr. W.A.S. Sarjeant and Dr. P.J. Currie, for the opportunity to conduct this research and I also thank them for their time and patience. The description of *Aquatilavipes* and *?Tricorynopus* prints were jointly undertaken with Dr. Sarjeant. Emendations to *Fuscinapeda* were completed by Dr. Sarjeant. Dr. M.J. Lockley deserves a special acknowledgment for encouraging my endeavours in the field of vertebrate ichnology and for allowing me the opportunity to work with him and Dr. C.A. Meyer on the ankylosaur footprint paper. I would also like to thank Dr. G. Leonardi, Dr. C.A. Meyer and Dr. E. Koppelhus for their time and assistance during the course of this research.

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Without the encouragement and support of my wife Dr. M.L. Gaynor, I would not have attempted to undertake graduate studies. I would also like to acknowledge the research contributions (in the form of muffins, fishing trips and good cheer) of my parents Raymond and Marlene, my sisters Kari (and her husband Edward) and Julie. I am very grateful to Bill and Barb Gaynor for their enthusiasm and hospitality and also to their daughters Kathy (and husband Daniel) and J'banet.

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LIST OF ABBREVIATIONS

RTMP = Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta

RBCMP = Royal British Columbia Museum of Palaeontology, Victoria, British Columbia

PMA = Provincial Museum of Alberta, Edmonton, Alberta

UALVP = University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton, Alberta.

CMN = Canadian Museum of Nature, Ottawa, Ontario

1.0 INTRODUCTION

1.1 Previous Vertebrate Palaeoichnological Work in Western Canada

The history of Early Cretaceous vertebrate palaeoichnology research in western Canada began in 1922 with F.H. McLearn's report of dinosaur footprints from the Gething Formation (Aptian) of the Peace River Canyon, in northeastern British Columbia (McLearn, 1923; 1931; Mossman and Sarjeant, 1983; Sternberg, 1931; 1932; 1933; Spalding, 1999). The result of C.M. Sternberg's research of this area led to the description of six new dinosaur ichnogenera and eight new ichnospecies (Sternberg, 1932).

Work on Lower Cretaceous dinosaur footprints was sporadic until the mid-1970's when studies recommenced on the Peace River ichnofauna (Sarjeant, 1981). This research led to the discovery and description of a new ichnogenus and ichnospecies of bird footprints (Currie, 1981), a new ichnospecies of hadrosaur footprint (Currie and Sarjeant, 1979) and a new ichnogenus and ichnospecies of marsupial mammal footprint (Sarjeant and Thulborn, 1986). Several trackways belonging to several ichnotaxa were mapped, and many original footprints as well as replicas were collected (Currie and Sarjeant, 1979).

These new discoveries shed light on the composition of a western Canadian Lower Cretaceous vertebrate ichnofauna which could then be compared to contemporaneous ichnofaunas worldwide (Lockley, 1991). Additional Lower Cretaceous footprint sites have since been reported, but most of these have yet to be documented satisfactorily (Currie, 1989; McCrea and Currie, 1998; McCrea *et al.*, 1998; McCrea *et al.*, in press, Appendix A).

1.2 Previous work on the Gates Formation

In 1989, an employee of the Smoky River Coal Mine, near the town of Grande Cache, Alberta, (Figure 1.1) reported the presence of footprints on a large sandstone block within the boundaries of the coal mine (South Pit Lake site) to the Royal Tyrrell Museum of Palaeontology (McCrea and Currie, 1998). Museum researchers sent to the coal mine to investigate confirmed the existence of multiple vertebrate tracksites, many of which were very extensive. They collected several original footprint specimens and made some replica casts as well (McCrea and Currie, 1998). In addition to the initial finds of numerous theropod footprints, it was soon realized that the Gates Formation contained the world's most significant record of ankylosaur footprints (McCrea and Currie, 1998; McCrea *et al.*, in press, Appendix A). Within a decade, several tracksites were identified in and around the property of the Smoky River Coal Mine. These tracksites represent the only large-scale exposures of vertebrate footprints in Canada since the flooding of the Peace River Canyon in 1979 (McCrea and Currie, 1998).

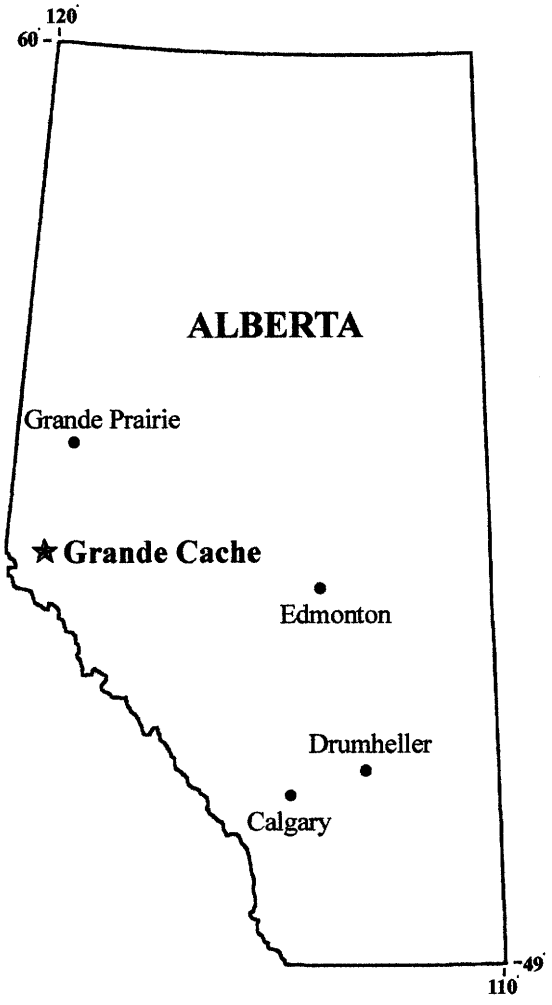

Figure 1.1. Location of research area.

1.3 Purpose of Study

Research on Lower Cretaceous vertebrates in North America has focused primarily on skeletal remains. The United States has several Lower Cretaceous

vertebrate skeletal sites: the Arundel Formation, Trinity Group, Cedar Mountain Formation, Cloverly Formation for example (Ostrom, 1970; Weishampel, 1990; Carpenter and Kirkland, 1998; Kranz, 1998; Lockley and Hunt, 1995); however, equivalent skeletal sites have not yet been documented from Lower Cretaceous strata of Canada. As a result, there are significant gaps in our understanding of the composition of Lower Cretaceous terrestrial vertebrate faunas of western Canada.

Vertebrate traces that are present in Lower Cretaceous sediments of western Canada can be used to fill in the gaps caused by the lack of skeletal material. These traces also provide glimpses of "living" terrestrial vertebrate communities in a way that is not possible with skeletal material: primarily of behavior and functional morphology (Lockley, 1986). Unlike skeletal remains, tracksites are *in situ* sedimentary structures (Sarjeant, 1990; Lockley, 1997a) and cannot be transported or reworked (however individual prints may be), and so give unequivocal evidence of the habitat that these extinct animals once frequented.

The numerous sites in the Gates Formation near Grande Cache, Alberta display an ichnofauna that consists of several ichnotaxa of dinosaurs (theropod, ?ornithopod and thyreophoran) as well as a modest diversity of avian and mammalian ichnotaxa. However, even a cursory survey of the tracksites reveals that the Smoky River ichnofauna is overwhelmingly dominated by *Tetrapodosaurus* footprints, which have been attributed to ankylosaurs (Carpenter, 1984; McCrea *et al.*, in press, Appendix A). This is significantly different than the ornithopod-theropod dominated ichnofauna from the Peace River Canyon. The Smoky River Ichnofauna has necessitated a modification to the view that the vertebrate palaeontology community at large had about the composition of Lower Cretaceous vertebrate ichnofaunas of Canada, hitherto based solely on the research of the Peace River ichnofauna. In North America, it had been assumed (with good reason) that Lower Cretaceous ichnofaunas of the Gulf regions of the United States (Texas) were dominated by the traces of theropods and sauropods

(Lockley, 1991; Currie, 1995). From Colorado to Alberta, the ichnofaunas were dominated by theropods and ornithopods (Lockley, 1991; Currie, 1995). With the recent research of the Smoky River ichnofauna, the vertebrate ichnofacies concepts proposed by Lockley *et al.*, (1994) will have to be modified to account for the presence of a *Tetrapodosaurus* (ankylosaur)-dominated ichnofauna within the lithological and palaeogeographical parameters that define the *Caririchnium* (ornithopod) ichnofacies.

The goals of this research were: 1) To record the precise location of known tracksites within the study area, and prospect for new tracksites; 2) To collect trackway and footprint measurements from one of these sites (W3 Main); 3) To collect representative specimens (original or replicas) of all vertebrate ichnotaxa found at the W3 Main site; 4) Make a study of this collected data to define the characteristics of the ichnofauna, including a census of the ichnofauna which could be compared with other contemporaneous ichnofaunas in North America; 5) Use the measurement data to determine the speeds of the track-makers; 6) Interpret behaviour from the observations made at the W3 Main and other tracksites.

2.0 GEOLOGICAL SETTING

2.1 Tectonics and Sea Level

The North American continent in the Albian was close to the same latitude that it occupies today (Barron, 1987; Smith *et al.*, 1994). There were significant differences in the positions of other continents relative to North America (Figure 2.1). Europe and Africa were positioned much closer to the east coast of North America, but were

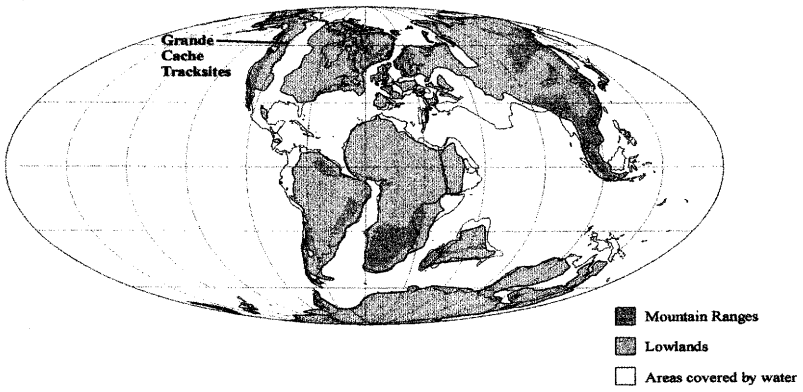

Figure 2.1. Approximate positions of continents and their coastlines in the Albian (Modified from Smith *et al.*, 1994), and the palaeogeographic location of the Grande Cache tracksites (from Lucas *et al.*, 1998). **Note:** the extent of the Lower Cretaceous Western Interior Seaway was variable through the Albian (see Figure 2.5 for a palaeogeographic reconstruction based on studies of the Gates Formation).

continuing to separate from the positions they had occupied before the breakup of the supercontinent, Pangaea, that had begun at the end of the Triassic (Osborne and Tarling, 1996). North America was divided by an epicontinental sea (the Lower Cretaceous Western Interior Seaway) that stretched from the Arctic Ocean to the Gulf of Mexico (Leckie and Smith, 1992). Western North America was an area of active orogenic

activity, resulting from collisions with other tectonic plates and their subsequent subduction (Leckie and Smith, 1992). North America may also have been connected to eastern Asia by a land bridge during this time. Eastern North America was on the passive continental margin and part of the mainland that included Greenland, which had not yet separated.

2.2 Depositional History and Geological Age of the Gates Formation

The research area is within the fold and thrust belt of the Inner Foothills of the Rocky Mountains (Langenberg *et al.,* 1987). There was a great deal of deformation of the strata due to tectonic uplift and folding, the majority of which occurred between the Campanian and the late Eocene (Kalkreuth and Langenberg, 1986; Langenberg *et al.*, 1987).

The sediments of the Gates Formation were deposited in the Western Canada Foreland Basin, part of the larger western North American Foreland Basin that extended from the Arctic Ocean to the Gulf of Mexico (Leckie and Smith, 1992). The Gates Formation was deposited during the second of three clastic depositional cycles in the Lower Cretaceous (Leckie, 1986; Leckie and Smith, 1992; Plint and Hart, 1988) and is one of many dinosaur track-bearing formations in the regressive phases of these sequences (Figure 2.2). The clastic deposits thicken in a westward direction, close to the sediment supply derived from the erosion of the Cordillera to the west (Leckie, 1986; Plint and Hart, 1988).

The Gates Formation forms the upper part of the Luscar Group, which includes, from oldest to youngest, the Cadomin Formation, the Gladstone Formation (Gething Formation equivalent) and the Moosebar Formation (Figure 2.3). The Luscar Group disconformably overlies the Upper Jurassic/Lowest Cretaceous Nikanassin Formation (Figure 2.4), the upper part of which is non-marine but the lower part marine (Langenberg *et al.,* 1987). The Luscar Group is overlain by the Shaftsbury (late Albian-

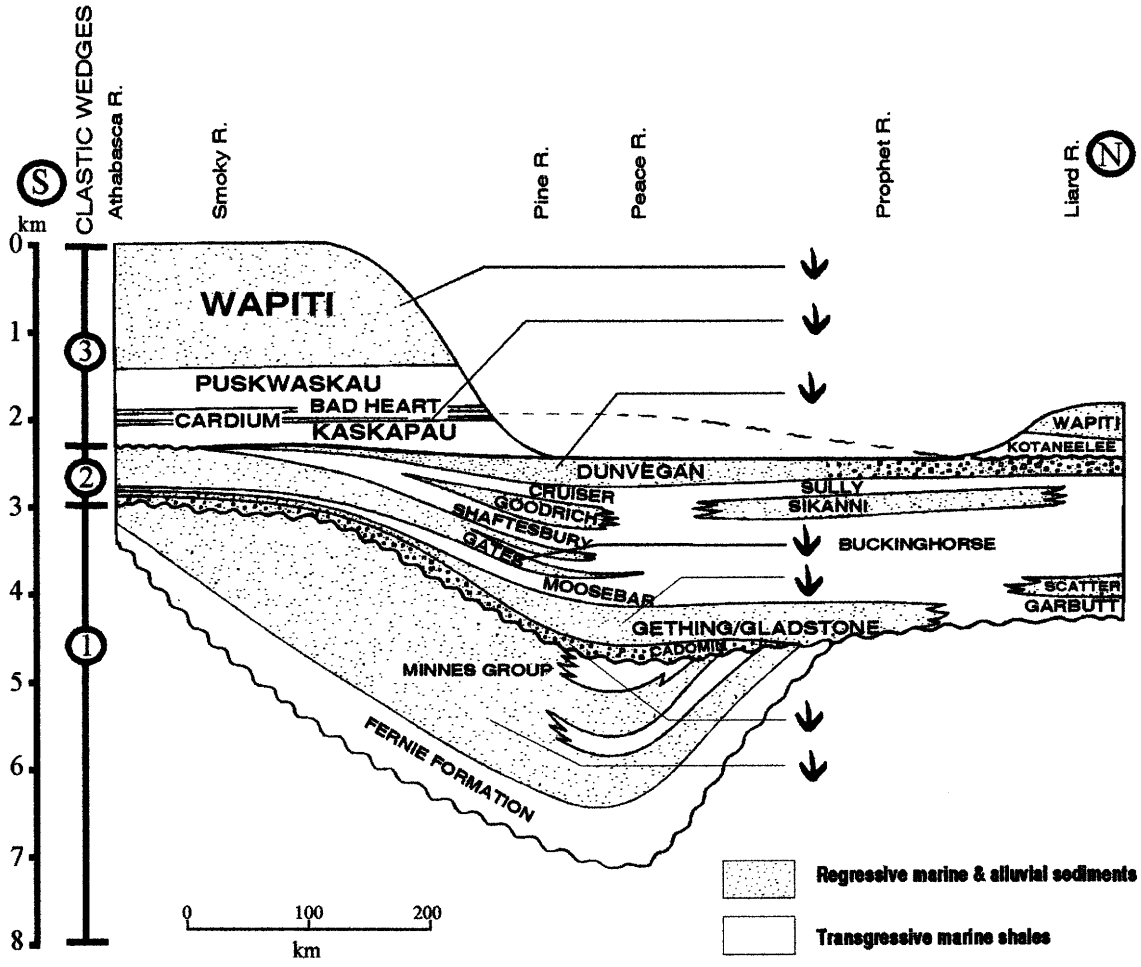

Figure 2.2. Simplified stratigraphic cross-section showing position of vertebrate trace-bearing formations in western Alberta and northeastern British Columbia (Modified from Plint and Hart, 1988). Data on footprint occurrences from Currie (1989), McCrea and Currie (1998) and McCrea *et al.*, (in press, Appendix A).

early Cenomanian), Dunvegan (Cenomanian) and Kaskapau (late Cenomanian) Formations (Langenberg *et al.*, 1987).

The Cadomin Formation (Neocomian-Albian) is composed primarily of thick conglomerate sequences which are interpreted as being pediment surfaces and alluvial fans (Langenberg *et al.*, 1987). The Gladstone Formation (early Albian for upper part) is composed of sandstone, shale and coal. The Moosebar Formation (early Albian) is mainly marine shales with ironstone and bentonite layers. The Gates Formation is divided into three members, the lowermost Torrens Member, the vertebrate track-

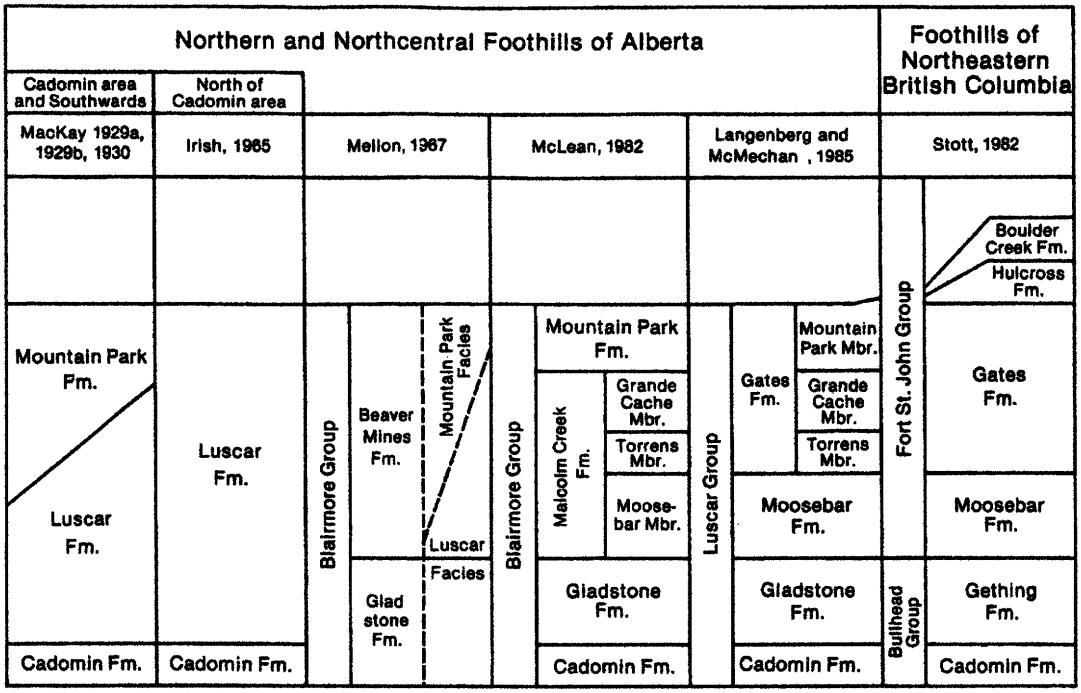

Figure 2.3. Stratigraphic nomenclature for the Lower Cretaceous in the northern and north-central Alberta Foothills and northeast British Columbia (From Langenberg *et al.*, 1987).

bearing Grande Cache Member and the uppermost Mountain Park Member (Figures 2.4). The Grande Cache Member is the source of the economic coal seams that are mined throughout central and western Alberta (Langenberg *et al.,* 1987). In the Smoky River Coal Mine, vertebrate footprints are found after the removal of the overlying Number Four Coal Seam within the Grande Cache Member (McCrea and Currie, 1998). Langenberg *et al.,* (1987) and Leckie and Smith (1992) interpret the palaeoenvironment as that of a coastal plain or deltaic complex (Figure 2.5). Leckie and Smith (1992) describe the climate in which the Gates sediments were deposited as "...a warm and humid-maritime setting along the inland of the coast in northeastern British Columbia and northwestern Alberta". This observation was based primarily on the presence of extensive coal seams within the Gates Formation. Research on the flora of the Gates Formation by Wan (1996) corroborated the interpretation of a warm climate with abundant rainfall, but he noted that this region may also have been seasonally cold, with temperatures dropping below -15°C. The age of the Grande Cache Member has been

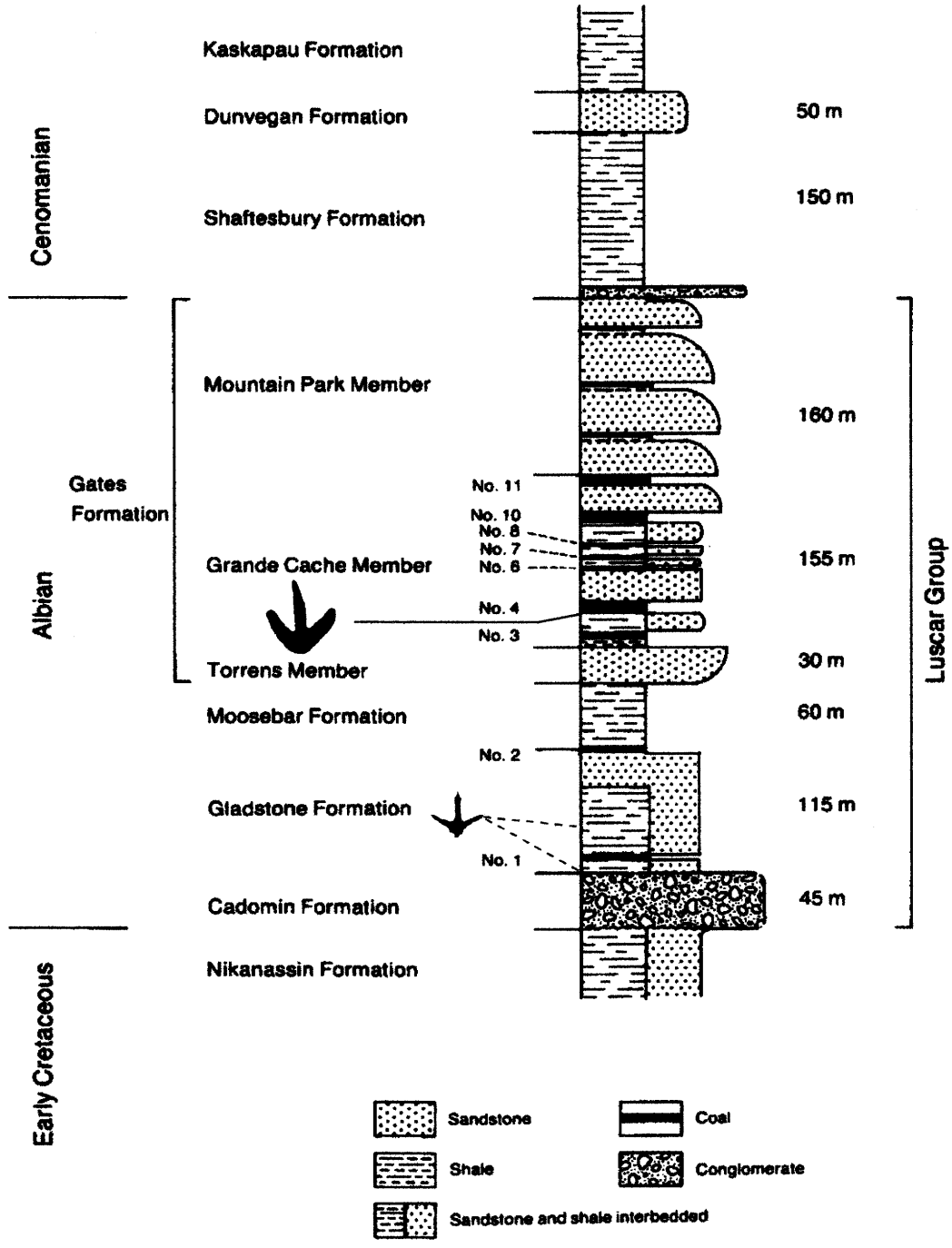

Figure 2.4. Simplified stratigraphic column with the position of coal seams and vertebrate footprints (Modified from Langenberg *et al.*, 1987)

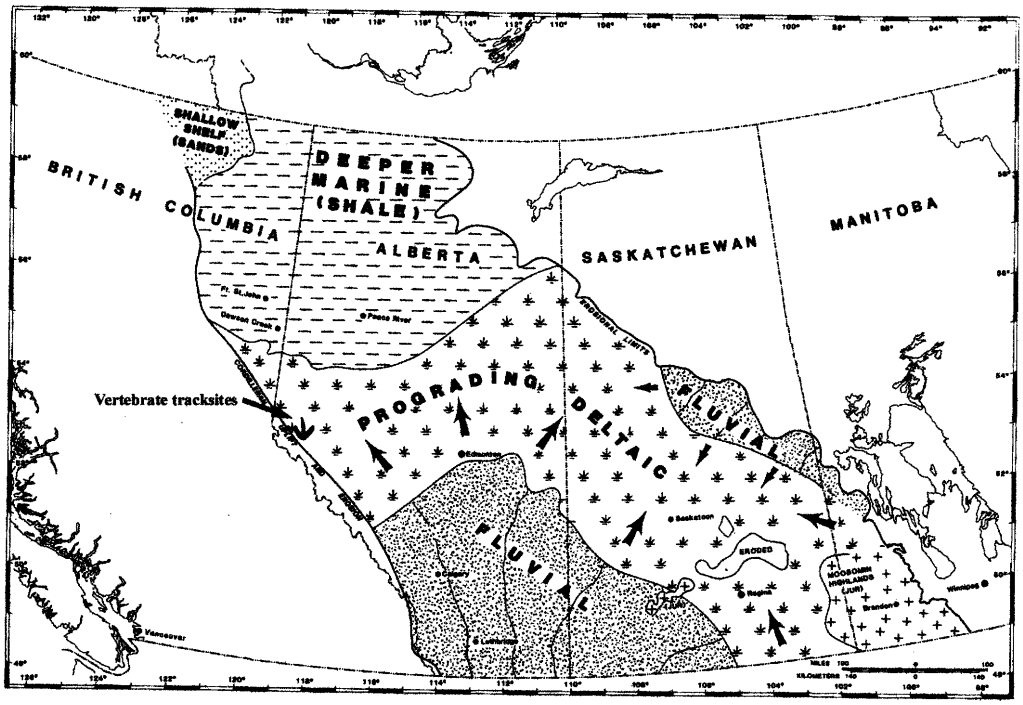

Figure 2.5. Palaeogeographic reconstruction of the Upper Mannville, Rex, General Petroleum, Waseca, Gates and Clearwater Formations and the Falher Member of the Spirit River Formation (Modified from Leckie and Smith, 1992). The location of the Gates Formation research area is indicated.

estimated as early Albian, based on the occurrence of the ostracode *Cytheridea bonaccordensis* (Langenberg *et al.,* 1987). Wan (1996) discussed microfaunal correlation in more detail and gave the Gates Formation a precise late early Albian age.

3.0 METHODS

A preliminary survey of the tracksites at the Smoky River Coal Mine in 1996, prompted further field trips intended to document the *Tetrapodosaurus* trackways from the 12 Mine South, A-Pit site before it was backfilled by Smoky River Coal Limited. However, this site collapsed in the summer of 1999 just when a research expedition was finally equipped to document it. With the loss of this site, research shifted to the documentation of the large W3 Main tracksite. The majority of the footprint data from the W3 Main site was collected in two weeks of field work in August-September, 1999. Observations on the many other Gates Formation sites (and one Gladstone Formation site) were made over the course of many visits to this area between 1996 and 1999.

Collection of original footprint specimens was out of the question in most cases; consequently, additional documentation included using liquid latex to make peels. The latex peel could then be used to prepare either plaster or fiberglass replicas. Representative samples of all vertebrate ichnotaxa present on the W3 Main footwall were gathered in this way. All collected materials (original and replicas) were accessioned at the Royal Tyrrell Museum of Palaeontology.

The W3 Main footprints were mapped using a grid constructed of several 1 m x 1 m squares. The baseline of the grid originated from the tip of the third digit of a prominent *Irenesauripus mclearni* footprint (Figure 5.3, grid A6/7). The baseline of the grid was constructed to be as closely parallel to the strike of the slope as possible (100°E, unadjusted). All of the footprints in the grid squares were mapped and every grid square was photographed individually. Over 1200 footprints were mapped within a 500m^2 grid area on the W3 Main footwall. Due to the angle of the track-bearing beds (about 60°), all documentation had to be gathered while attached to a harness and a

series of static 100 m ropes. A significant period of time had to be expended preparing the site to make it safe for this research.

Documentation was carried out by taking measurements of *in situ* footprints and trackways. Footprint and trackway measurements (Figure 3.1) were taken after Leonardi (1979) and Thulborn (1990), as was the terminology used to describe various aspects vertebrate palaeoichnological research. Some of these terms are defined below:

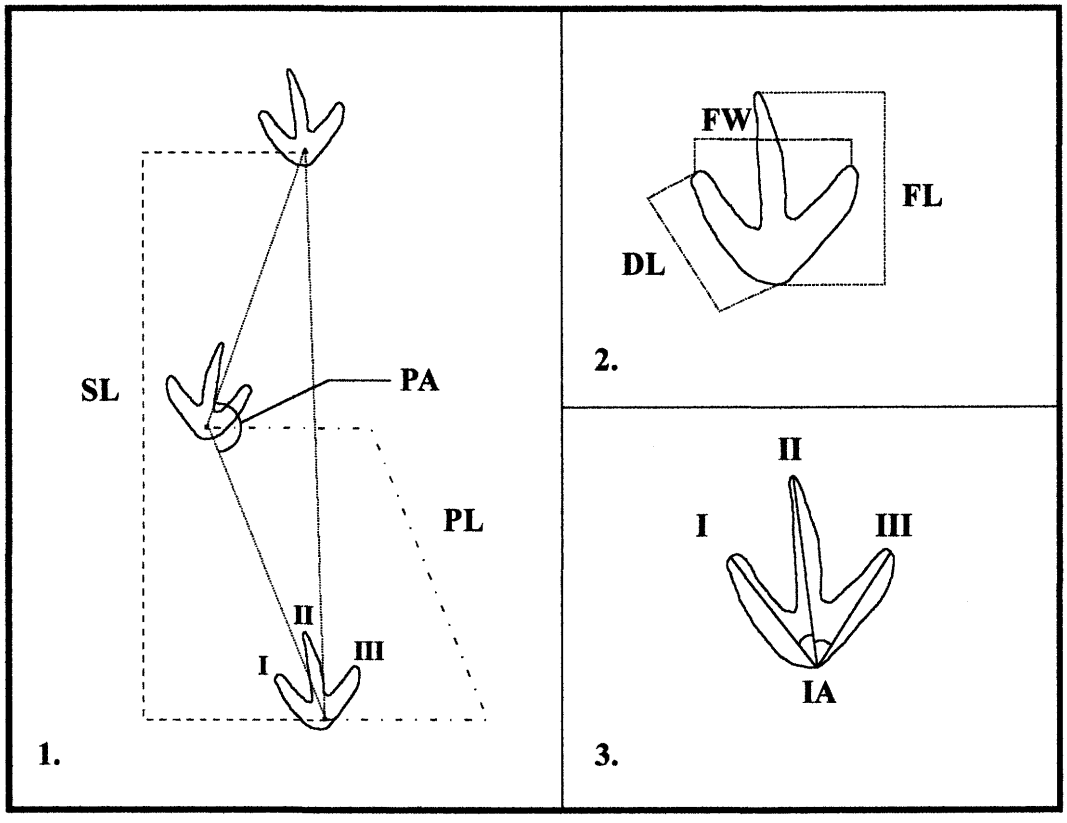

Figure 3.1.1-3: Footprint and trackway measurement methods after Thulborn (1990). 1, Trackway measurements: SL = Stride Length, PL = Pace Length and PA = Pace Angulation). 2, Footprint measurements: FL = Footprint Length, FW = Footprint Width and DL = Digit Length. 3, Digit divarication: IA = Interdigital Angles

1. A *trackway* is a series of footprints. Trackway measurements included *stride length*, *pace length* and *pace angulation* (Figure 3.1.1). Stride and pace measurements were taken using the center of the footprints in question, not from the tips (length is too

variable). In the footprints of bipeds the measurement was taken behind digit III, in quadrupeds between digits II and III of the pes.

2. A *footprint* is a single impression of a foot, isolated or forming part of trackway. The use of *track* as equivalent to footprint is common in North America; however, in Europe (and indeed by hunters in North America), this term is always used to refer to a series of footprints (equivalent to "trackway"). To avoid confusion, the use of the term "track" should be avoided. Footprint measurements included *footprint length* and *footprint width* (Figure 3.1.2).

3) *The length of the individual digits* is normally measured between the digit tip and its point of contact with the metatarsal pad. This is the most correct approach, but it is difficult to apply to shallow prints or under erratic lighting conditions. Digit length may be more readily taken by measuring from the tip of the digit impression, along the digital axis, to the posterior margin of the footprint (Figure 3.1.2). All digital length measurements were taken in this fashion.

4) The *interdigital angle (digit divarication)* is the angle between the axes of two digits (Figure 3.1.3). *Total divarication* is the angle between the outermost digits. In bipedal dinosaurs and birds these are usually digits II and IV.

Footprint and trackway data collected at the W3 Main site was used to calculate the size and velocity of the various track-making animals. Speed calculations were based on Alexander (1976).

$u = 0.25\, g^{0.5}\lambda^{1.67}h^{-1.17}$ $\qquad u = \frac{0.782\lambda^{1.67}}{h^{1.17}}$ m/s (3.6) = km/h

u = velocity of travel m/s-1

g = acceleration of free fall (9.8m/s-1)

λ = stride length (m)

h = hip height (m)

Hip height calculations were based on the allometric ratios of Thulborn (1990), with the exception of the *Tetrapodosaurus* footprint-producing animal where 4FL was used instead (Alexander, 1976).

Allometric Hip Height Calculations

Bipeds

Small Theropods (FL < 25cm): $h \approx 3.06FL^{1.14}$ (*Gypsichnites*, *Columbosauripus*)

Large Theropods (FL > 25cm): $h \approx 8.60FL^{0.85}$ (*Irenesauripus*, *Columbosauripus* and *Gypsichnites*)

Theropods in general: $h \approx 3.14FL^{1.14}$

Ornithomimids: $h \approx 3.49\ (1.5FL)^{1.02}$ (*Irenichnites*)

Small Ornithopods (FL<25cm): $h \approx 3.97FL^{1.08}$

Large Ornithopods (FL>25cm): $h \approx 5.06FL^{1.07}$

Ornithopods in general: $h \approx 3.76FL^{1.16}$

Quadrupeds

Ankylosaurs: $h \approx 4FL$ (*Tetrapodosaurus*)

Based on the studies of the footprints of modern animals, Alexander (1976) found that the ratio of stride length (SL) to height at the hip (h) could be used to determine the gait of extinct animals. Trackways with ratios under 2.0 were produced by animals walking at a normal, unhurried pace. At ratios between 2.0 and 2.9, the animals were proceeding at a trot. Ratios of 2.9 or greater were produced by running animals.

4.0 SYSTEMATIC PALEONTOLOGY

Superorder Dinosauria Owen, 1842

Order Saurischia Seeley, 1887

Suborder Theropoda Marsh, 1881

Ichnogenus ***Irenesauripus*** Sternberg, 1932

Original Diagnosis: "Large; semidigitigrade; functionally tridactyl; toes well separated; heel of variable width, but always completely impressed; weight borne equally by the three toes and the metatarsal pad; phalangeal pads not well defined; claws acuminate; no manus or caudal impressions." (Sternberg 1932, p. 62).

Emended Diagnosis: Large; bipedal; semi-digitigrade; heel of variable width; functionally tridactyl footprint is always mesaxonic (digit III is the principal digit); digit I is rarely impressed. Digit impressions are well separated; phalangeal pad and claw impressions are visible on better preserved natural moulds — three (two phalangeal pads; one claw) on digit II, four on digit III, and four to five may be visible on digit IV (Figure 4.1.1); claws acuminate. The position and pattern of the digital pads and claws matches the phalangeal formula of carnosaurs (Figure 4.1.2) which is 2:3:4:5 (Molnar *et al.*, 1990).

Type Ichnospecies: Irenesauripus mclearni Sternberg, 1932. Gething Formation (Early Cretaceous: Aptian) eastern British Columbia.

Remarks: The diagnosis of this ichnogenus is emended to take into account the presence of phalangeal pad impressions, which are seen in some footprint specimens from the W3 Main site near Grande Cache, Alberta.

Description: See Sternberg (1932 p.62)

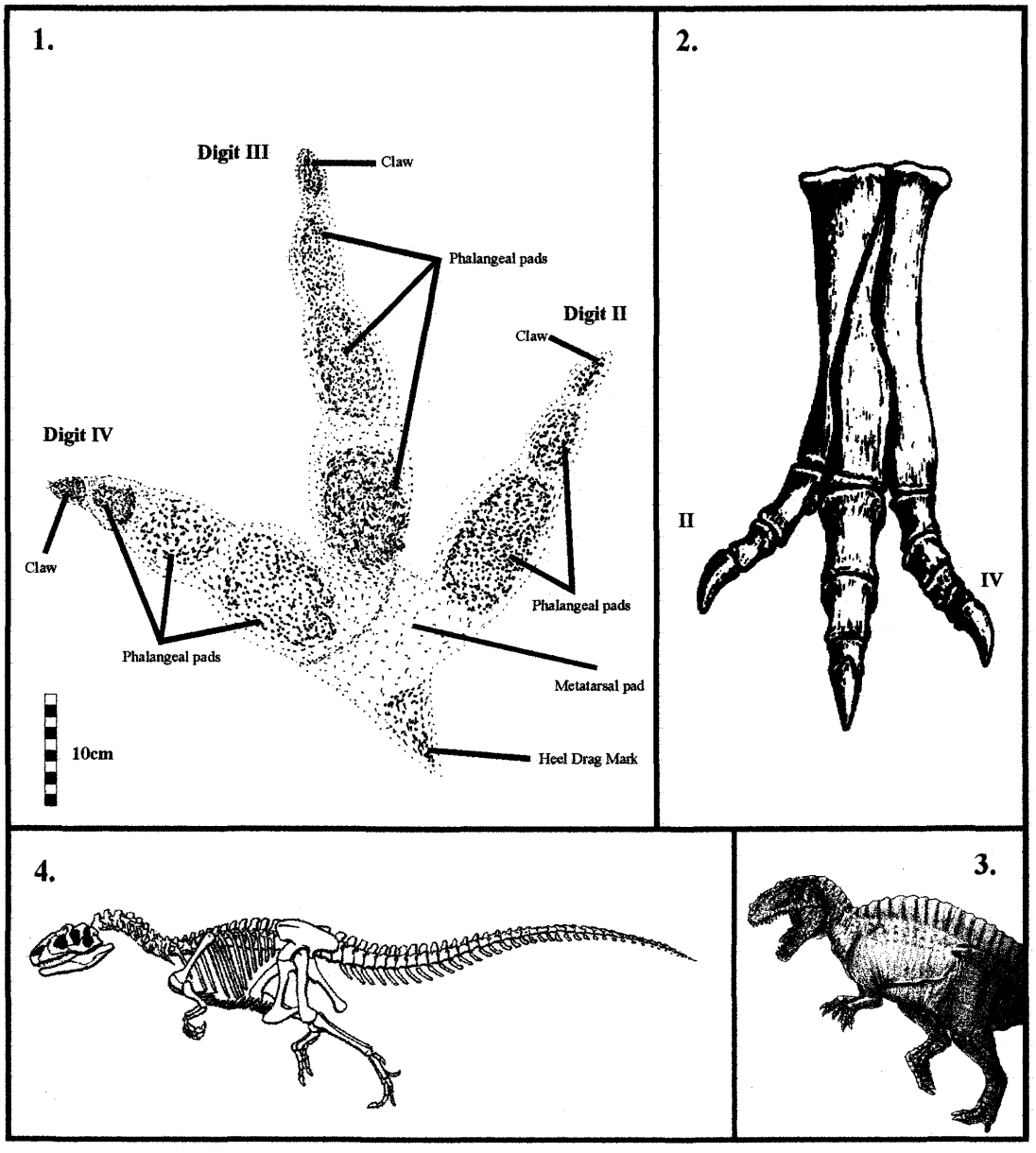

Figure 4.1.1-4: *Irenesauripus mclearni* Sternberg, 1932; Morphology of *I. mclearni* footprint compared to a carnosaur foot. 1, Illustration of *I. mclearni* footprint (left pes) from a replica cast (TMP 99.49.4) from grids A6/7 (Figure 5.3); 2, Illustration of a carnosaur foot (*Allosaurus*); reversed right pes (about 71 cm long), modified from Thulborn (1990). 3, Illustration of *Acrocanthosaurus atokensis* from Lessom and Glut (1993). 4, Skeletal illustration of *Allosaurus* from Fastovsky and Weishampel (1996).

Materials: Numerous specimens from the W3 Main tracksite.

Irenesauripus mclearni Sternberg, 1932.

(Figures 4.1.1-4, 4.2.1-3 and 4.3; Tables 1 and 2)

Original Diagnosis: "The tracks vary from 11 to 16 inches in length [27.9 to 40.6 cm]. Normally they are almost in a direct line and the stride [pace] is approximately three times the length of the track, but these characters vary with the nature of the surface and the speed of the animal.

The longest stride [pace] in the trackway of sixteen tracks, of which the type specimen is a part, was 1,065 mm and the average 940 mm. In this, as well as in another trackway of this species (Plate I), there is a depression at the back of imprint that appears to have been made by the dragging of the central toe as the foot was coming to rest. In other trackways of this species this "drag" is not shown.

The weight was borne equally by the three toes and the metatarsal pad or the so-called heel. The heel is moderately narrow. The toes are separated well back and there is no indication of a web or extensive pad. They taper gradually from near the proximal ends and terminate in rather sharp claws. Divarication of digits II and III, 37 degrees; of III and IV, 33 degrees." (Sternberg 1932, p. 62).

Description: See Sternberg (1932, p. 62).

Holotype: NMC 8548 (partial trackway with three footprints; original natural mould) lodged at the Canadian Museum of Nature, Ottawa, Ontario (Currie 1978, unpublished field notes).

Dimensions: See Sternberg (1932, p. 62). *Range of Dimensions:* see Table 1.

Discussion: The large tridactyl prints found at Grande Cache are very similar to *Irenesauripus mclearni* (Table 1; Figure 4.2.1-3). Sternberg (1932) described three ichnospecies within the ichnogenus *Irenesauripus*: *I. mclearni*, *I. acutus* and *I. occidentalis* from the Peace River Canyon (Gething Formation). Currie (1995) compared the similarity of length, width and divarication measurements of *I. occidentalis* to the ornithopod ichnogenus *Amblydactylus* and found them to be nearly

Figure 4.2.1-3: *Irenesauripus mclearni* footprints from the W3 Main Tracksite. 1, *Irenesauripus mclearni* trackway. The position of the two prints in the lower left of the photograph are plotted in Figure 5.3 (Grid K4 and L6). 2, Right pes from trackway in Figure 4.2.1 (arrowed). 3, Photograph of the left pes footprint illustrated in figure 4.1.1 and plotted in Figure 5.3 (Grid A 6/7).

identical. He also compared the abundance of *Amblydactylus* prints to the single occurrence of four prints of *I. occidentalis* and concluded that *I. occidentalis* prints were likely to be a morphological variant of *Amblydactylus*. These morphological differences can be caused by variations in substrate consistency. *I. occidentalis* is considered to be synonymous with *Amblydactylus* (Currie, 1995).

Divarication measurements and digital proportions of the Grande Cache prints (Table 1) fit very well with *I. mclearni*, (Table 2) but they are slightly larger than those that Sternberg originally described from the Peace River Canyon (1932). The Grande Cache prints are similar to *I. acutus* in footprint length, but digits II and III of *I. acutus* are more deeply impressed than digit IV which is not a feature that has been observed in the *Irenesauripus* footprints found at Grande Cache. It should be noted that Sternberg (1932) reported only one *I. acutus* trackway from his study of the Peace River Canyon, among numerous *I. mclearni* trackways. However, more recent studies have recognized at least five *I. acutus* trackways (Currie, 1995).

The Grande Cache footprints resemble *I. mclearni* more closely than *I. acutus*

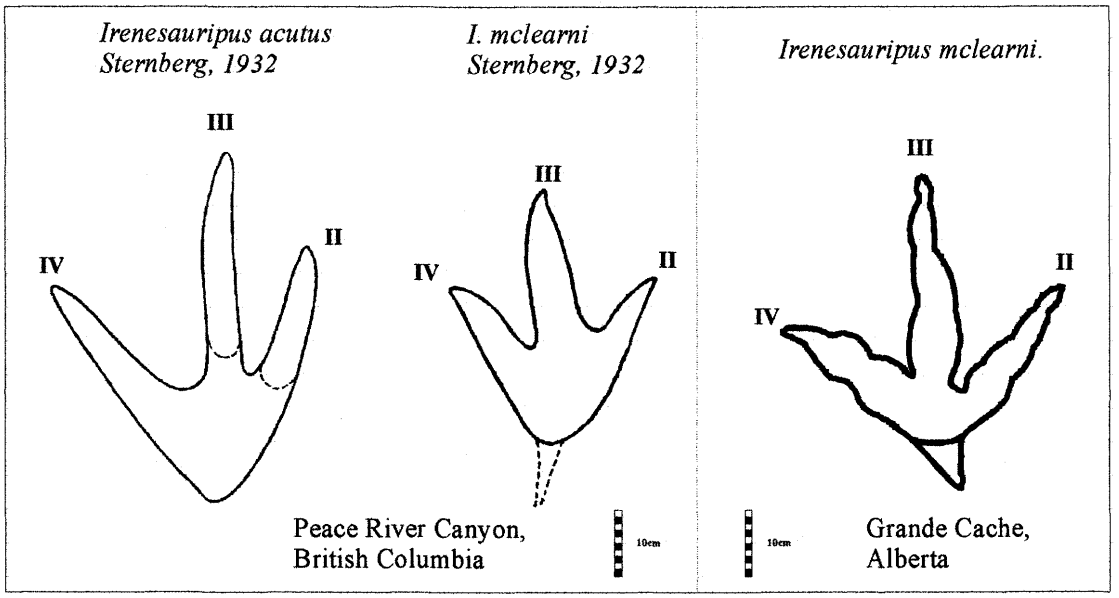

Figure 4.3. Comparison between large tridactyl prints from Grande Cache, Alberta and *Irenesauripus mclearni* and *I. acutus* from the Peace River Canyon, British Columbia.

1.0 INTRODUCTION

1.1 Previous Vertebrate Palaeoichnological Work in Western Canada

The history of Early Cretaceous vertebrate palaeoichnology research in western Canada began in 1922 with F.H. McLearn's report of dinosaur footprints from the Gething Formation (Aptian) of the Peace River Canyon, in northeastern British Columbia (McLearn, 1923; 1931; Mossman and Sarjeant, 1983; Sternberg, 1931; 1932; 1933; Spalding, 1999). The result of C.M. Sternberg's research of this area led to the description of six new dinosaur ichnogenera and eight new ichnospecies (Sternberg, 1932).

Work on Lower Cretaceous dinosaur footprints was sporadic until the mid-1970's when studies recommenced on the Peace River ichnofauna (Sarjeant, 1981). This research led to the discovery and description of a new ichnogenus and ichnospecies of bird footprints (Currie, 1981), a new ichnospecies of hadrosaur footprint (Currie and Sarjeant, 1979) and a new ichnogenus and ichnospecies of marsupial mammal footprint (Sarjeant and Thulborn, 1986). Several trackways belonging to several ichnotaxa were mapped, and many original footprints as well as replicas were collected (Currie and Sarjeant, 1979).

These new discoveries shed light on the composition of a western Canadian Lower Cretaceous vertebrate ichnofauna which could then be compared to contemporaneous ichnofaunas worldwide (Lockley, 1991). Additional Lower Cretaceous footprint sites have since been reported, but most of these have yet to be documented satisfactorily (Currie, 1989; McCrea and Currie, 1998; McCrea *et al.*, 1998; McCrea *et al.*, in press, Appendix A).

(Figure 4.3), but it is possible that *I. mclearni* and *I. acutus* are synonymous since the morphological differences could be the result of different substrate consistencies. Gatesy *et al.*, (1999) documented a wide spectrum of theropod footprint preservation in the Triassic Fleming Fjord Formation of Greenland. On one side of the spectrum were well-preserved tridactyl prints, easily identifiable as belonging to the ichnogenus *Grallator*. On the opposite side of the spectrum, were elongate prints with the digits reduced to "...smooth channels constricting to narrow slits" (Gatesy *et al.*, 1999). Several footprints with intermediate morphologies were found, indicating that one type of track-maker was responsible for producing the different footprint morphologies (variants of *Grallator*). The controlling factor was the consistency of the substrate the track-maker had walked upon.

In the case of *Irenesauripus* footprints, on relatively firm substrates a large theropod might make footprints resembling *I. mclearni*. However, the same theropod stepping on less well-consolidated substrates (mud or very wet sand) might produce footprints with longer, narrower digit impressions closely resembling *I. acutus*. The footprints from Grande Cache appear to be somewhat intermediate between the two forms, indicating a substrate intermediate between unconsolidated mud and firm, dry ground.

With the inclusion of the Grande Cache data, *Irenesauripus mclearni* footprints now vary in length between 27.9 cm to 49.5 cm. However, *Irenesauripus glenrosensis* prints found in Texas are up to 66 cm long (Langston, 1974; 1979). Based on the measurements from two trackways at Grande Cache, the longest stride is 313.0 cm and the longest pace is 161.5 cm (Table 1). A posterior projection on the "heel" is also seen in some Gates Formation specimens and is most likely a dragging trace of the posterior pad of digit IV (Martin Lockley, pers. comm. 1999). This posterior trace was absent in some trackways from the Peace River Canyon (Sternberg, 1932): Irby (1995) considered that such features might indicate a form of sexual dimorphism.

Irenesauripus footprints comprise less than 2% of the total ichnofauna studied at the W3 Main site (Gates Formation) and are only found on two or three other sites in the Grande Cache area. In contrast, *Irenesauripus* prints are found at multiple levels in the Peace River Canyon (Gething Formation) and comprise a significant proportion of the total ichnofauna (Sternberg, 1932; Currie, 1995).

From the size of the footprints and trackways, as well as the presence of large claws, the track-maker was most probably a large theropod. The length and slenderness of the digits suggests that the prints were made by a gracile carnosaur, such as an allosaurid or megalosaurid, rather than a robust carnosaur which would have shorter and broader digits (Moratalla *et al.*, 1988). It has been assumed that the track-maker was *Acrocanthosaurus atokensis* (Langston, 1997; Jacobs, 1997), whose skeletal remains occur in the Trinity Group (Aptian-Albian) of Texas (Figure 4.1.3). Fragmentary remains of large theropods, from other contemporaneous strata in the United States, have also been referred to *Acrocanthosaurus* (Ostrom, 1970; Weishampel, 1990; Lipka, 1998). However, Harris (1998) points out that many of these fragmentary remains are not really attributable to *Acrocanthosaurus* and that no diagnostic material of *Acrocanthosaurus* has been found in sediments outside of the Trinity Group. If the *Irenesauripus* track-maker was not *Acrocanthosaurus*, then it was a carnosaur (allosaurid) of similar size and form (Figure 4.1.4).

Superorder Dinosauria Owen, 1842

Order Saurischia Seeley, 1887

Suborder Theropoda Marsh, 1881

Ichnogenus ***Columbosauripus*** Sternberg, 1932

Original Diagnosis: "Small; bipedal; semi-digitigrade; functionally tridactyl; toes well spread and carrying the main weight; proximal ends of toes enclosed in pad or web; digit II not cut away from metatarsal pads; toes tapering and terminating in long, sharp

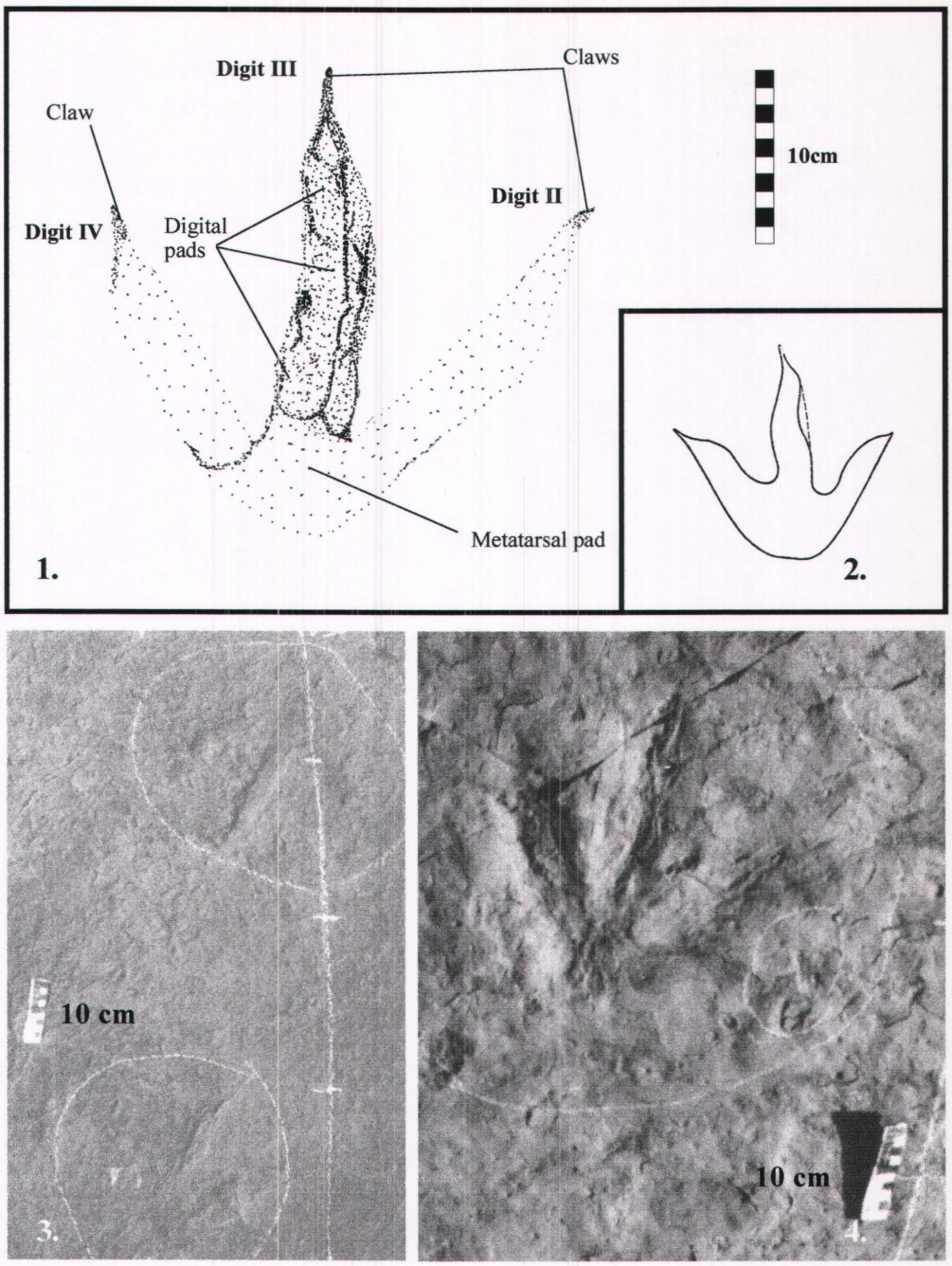

Figure 4.4.1-4: *Columbosauripus ungulatus* Sternberg 1932; 1, Left pes illustration of *C. ungulatus* drawn from a replica cast (TMP 98.89.6) from Grid K7. 2, Sternberg's (1932) illustration of *C. ungulatus* holotype (NMC 8551); same scale as Figure 4.4.1. 3, *C. ungulatus* footprint illustrated in figure 5.3 (Grid E23). 4, *C. ungulatus* footprints from figure 5.3 (B29).

claws; heel well rounded; phalangeal pads not well shown." (Sternberg 1932, p. 65)

Emended Ichnogenus Diagnosis: Small to medium footprints; bipedal; semi-digitigrade; functionally tridactyl; digits are well-spread; digits taper at distal ends to long, sharp claws (Figure 4.4.2); in some prints, at least three faint phalangeal pads are seen in digit III (Figure 4.4.1); All digits attached to the metatarsal pad.

Type Ichnospecies: Columbosauripus ungulatus Sternberg, 1932. Gething Formation (Early Cretaceous: Aptian), eastern British Columbia.

Remarks: The diagnosis of this ichnogenus is emended to take into account the presence of phalangeal pad impressions, which are seen in some footprint specimens from the W3 Main site near Grande Cache, Alberta.

Columbosauripus ungulatus Sternberg, 1932

(Figure 4.4.1-4; Table 3)

Original Diagnosis: "The imprint shows very good detail, but no distinct phalangeal pads. The digits are well separated in their distal halves. The pads of the proximal phalanges and the metatarsals seem to have been merged into one big pad, as there is no sign of separation between them. The heel is broadly rounded, but only faintly impressed. The digital impressions to near their distal ends taper very gradually, beyond this they narrow abruptly and terminate in long, vertical slits, which must have been made by long, narrow claws. Divarication of digits II and III, 38 degrees; of III and IV, 39 degrees." (Sternberg 1932, pp. 65-67).

Emended Diagnosis: An ichnospecies of *Columbosauripus* in which the footprint length to width ratio is low, averaging approximately 1.10, but may be as high as 1.35 or as low as 0.88. Digits II and IV are of almost equal length. Divarication between digits II and III, and between III and IV are almost equal (around 40°). There is a slight curvature in digit III that begins about half way between the terminus of the digit and where it unites in the metatarsal pad.

Materials: Numerous specimens from the W3 Main tracksite.

Description: See Sternberg (1932, p. 65-67) for details.

Holotype: NMC 8551 (original natural mould) lodged at the Canadian Museum of Nature, Ottawa, Ontario (Currie 1978, unpublished field notes).

Dimensions: See Sternberg (1932, p. 65-67) for details. *Range of Dimensions:* See Table 3.

Remarks: The diagnosis of this ichnospecies is emended to include footprint length/ width ratios and the curvature of digit III.

Discussion: The Grande Cache footprints correspond well with Sternberg's (1932) monospecific ichnotaxon *Columbosauripus ungulatus*. The rounded heel of the W3 prints is similar, as is the flexibility of the third digit. There is similarity in the digits, which taper very gradually and narrow to long, vertical slits (claws). The outer digits in the Peace River and W3 Main *C. ungulatus* prints are nearly equal in length. The only observable difference is that the Gates Formation *C. ungulatus* prints are more than twice as large as the ones that Sternberg described from the Gething Formation, and the stride and pace are correspondingly greater (Table 3).

The presence of claw impressions suggests that the trace-maker was a theropod, possibly a coelurosaur or an ornithomimid (Thulborn, 1990). One problem with identifying the makers of mid-sized theropod footprints is that a wide variety of theropod taxa are capable of producing them. Thulborn (1990) uses the detached digit II impression in the smaller *Irenichnites* footprints to identify that particular trace-maker as an ornithomimid. In ornithomimids, digit II is attached higher up on the foot than the other weight-bearing digits and may have been incompletely impressed, causing the observed separation of digit II (Thulborn, 1990). Such a separation of digit II is not seen in specimens of *Columbosauripus*, making it more likely that the trace-maker was another form of medium-sized theropod. Some of the better trackways of *Columbosauripus* were above the main study area on the W3 Main tracksite and also at

the W2 tracksite. Future studies may permit a more precise identification of the *Columbosauripus* trace-maker.

Columbosauripus footprints have also been found in the Dunvegan Formation (Cenomanian) of northeastern British Columbia (Storer, 1975) and in Algeria (Haubold, 1971).

Superorder Dinosauria Owen, 1842

Order ?Saurischia Seeley, 1887

Suborder ?Theropoda Marsh, 1881

Ichnogenus ***Gypsichnites*** Sternberg, 1932

Original Diagnosis: "Bipedal; semidigitigrade; tridactyl; heel broadly rounded and complete; foot short and broad; toes broad, partly enclosed in pad or web, and terminating in bluntly pointed hoofs.

Emended Diagnosis: The footprints of a tridactyl, semi-digitigrade biped. The footprint is longer than wide. Some observed specimens display lateral digits that are detached from the rest of the footprint. Digits are broad with distal portions often displaying distinct swelling, especially digit III. Distinct terminal claws are evident on some specimens of this ichnogenus which cannot be classified as "bluntly pointed hoofs".

Type Species: Gypsichnites pascensis Sternberg 1932. Gething Formation (Early Cretaceous: Aptian), eastern British Columbia.

Remarks: This ichnogenus is emended to include the separation of lateral digits from the rest of the footprint as well as the presence of terminal claws in some specimens.

Gypsichnites pascensis Sternberg, 1932

(Figures 4.5.1-3 and 4.6.1-3; Tables 4a-d)

Original Diagnosis: "The type (Plate IV, Figure 1, and Figure 6) shows very good

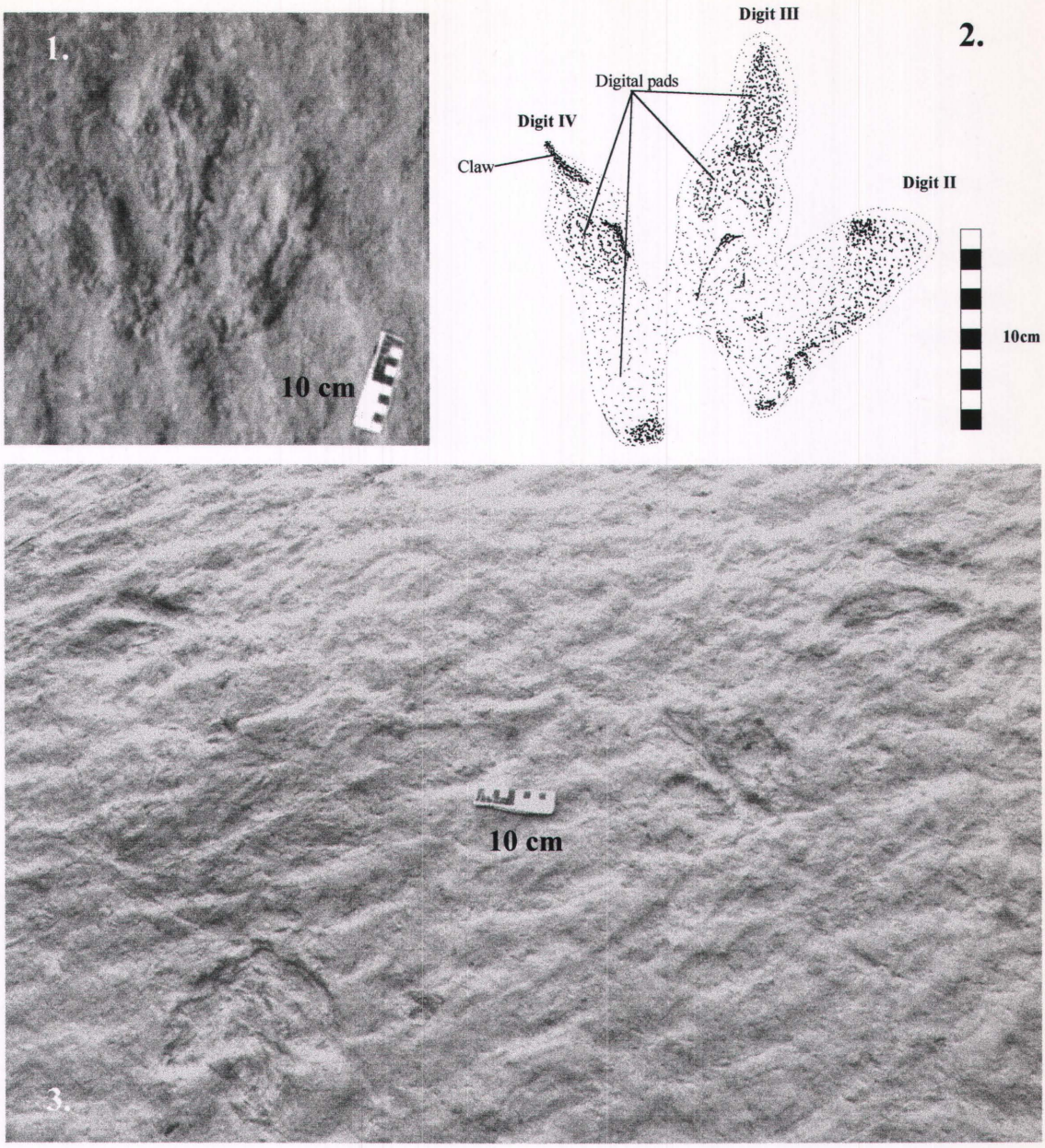

Figure 4.5.1-3: *Gypsichnites pascensis* Sternberg (1932); 1, Left pes (Figure 5.3; Grid C/D 2). 2, Illustration of left pes taken from a replica cast (TMP 98.89.8) from Grid I13 (Figure 5.3). 3, Four pes prints (Figure 5.3; Grid C/D3/4).

outline, but no phalangeal pads. All the toes are very broad and end in bluntly pointed hoofs. Digits II and IV are strongly divergent, point outward at their distal ends, but are free for only about one-half of their length. The proximal portions of the toes were doubtless enclosed in a pad or web. In the type, digit III is more deeply impressed than

the others, but in the paratype the three toes seem to have carried the weight about equally. Digit III is broadest near the distal extremity, whereas the others taper gradually. In the type, a poorly preserved second track indicated a stride...[of]...slightly more than three times the length of the track. In the paratype, the length of the stride relative to the length of the tracks is slightly greater. The tracks are almost in a straight line but point slightly outward from the line of march." (Sternberg 1932, pp. 70-72).

Emended Diagnosis: An ichnospecies of *Gypsichnites* with a few specimens in which there are phalangeal pad impressions preserved (Figure 4.5.2), most prominently in digit

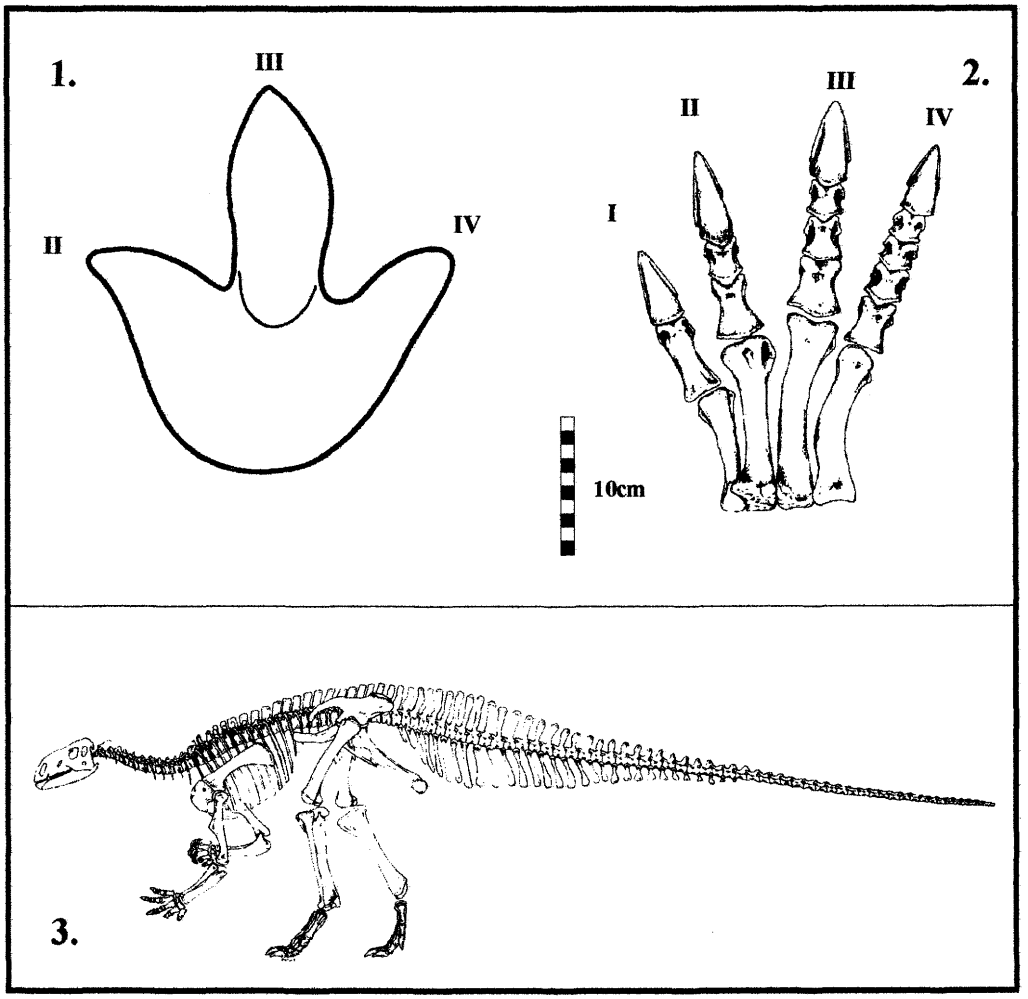

Figure 4.6.1-3: 1, Pes print (reversed) of *Gypsichnites pascensis* holotype (Sternberg,1932). 2, Illustration of right pes of *Tenontosaurus tilletti*; modified from Forster (1990). 3, Reconstruction of *T. tilletti*; from Forster (1990).

III. Some *Gypsichnites* footprints appear to be very theropod-like, with one or both outer digits being separated from digit III (Figure 4.5.2). However, this effect may be caused by the quality of the substrate the animal was walking on, a bit firmer than the substrates the other typical *Gypsichnites* were formed upon perhaps. Some footprint specimens show evidence of claw impressions (Figure 4.5.2). The footprint length/ width ratios range between 1.1-1.52 with an average of 1.19, which is similar to Sternberg's (1932) holotype (FL/FW = 1.03) and falls within the ornithopod range suggested by Moratalla *et al.*, (1988).

Description: See Sternberg (1932, pp. 70-72) for details.

Holotype: NMC 8553 (single footprint: original natural mould) lodged at the Canadian Museum of Nature, Ottawa, Ontario (Currie 1978, unpublished field notes).

Dimensions: See Sternberg (1932, pp. 70-72). *Range of Dimensions:* (See Tables 4a-d).

Materials: Numerous specimens from the W3 Main tracksite.

Remarks: This ichnospecies is emended to include the presence of phalangeal pads which have been observed in some specimens as well as observations of footprint length/width ratios.

Discussion: Many of the W3 Main *Gypsichnites pascensis* prints conform well with Sternberg's (1932) original diagnosis (Figure 4.5.1, see 4.6.1 for comparison), but others within the same trackway differ significantly (Figure 4.5.2 and 4.5.3 - center right), due to variation in substrate consistency and dynamics of locomotion (Thulborn and Wade, 1989). In Sternberg's (1932) original diagnosis, he tentatively referred *Gypsichnites* prints to the theropod ichnofamily Eubrontidae, but felt that the prints had been made by plant-eating ornithopods. The FL/FW ratios of *Gypsichnites* footprints from the Gates Formation (W3 Main) suggest that they were produced by an ornithopod dinosaur rather than a theropod (Moratalla *et al.*, 1988; Thulborn, 1990). However, all of the tridactyl footprints attributable to bipedal dinosaurs from this study of the Gates Formation are distributed above and below the point that Moratalla *et al.*, (1988) suggest for the

division between ornithopods and theropods (theropod >1.25> ornithopod). Footprint length/width calculations are not diagnostic for distinguishing the footprints of ornithopods and theropods, at least not for the Gates Formation footprints. Other morphological traits must be relied upon to make the distinction between ornithopod footprints and those produced by theropods.

Most of the prints have digital extremities that are bluntly rounded, which is an ornithopod trait (Thulborn, 1990). The presence of claws in some footprints might point to the trace-maker as belonging to the Theropoda. However, the presence of claws does not automatically make this a theropod ichnotaxon. The hypsilophodonts are primitive ornithopods that do possess claws (Sues and Norman, 1990) and probably made footprints that could easily be mistaken for theropods. However, Thulborn (1990) observed that the footprints of small ornithopods may have narrow claws, "...but these are neither so slender nor so sharply pointed as the claws of small theropods". Most *Gypsichnites* prints do not show terminal claw marks, but enough do to raise the question of its affinity, which has traditionally assumed to be ornithopod. The identification of certain footprints as either theropod or ornithopod may be difficult (Thulborn, 1990; Schult and Farlow, 1992; Farlow and Chapman, 1997).

Gypsichnites footprints have been attributed to the ornithopod genus *Tenontosaurus* (Langston, 1997), whose skeletal remains are found in the Lower Cretaceous Cloverly Formation of Montana and Wyoming (Ostrom, 1970); these are the closest contemporaneous skeletal sites to these tracksites. *Tenontosaurus* is closely related to the Iguanodontia (Sereno, 1986), but is interpreted as being capable of only limited quadrupedal locomotion (Figure 4.6.3), for food gathering perhaps. It would likely have utilized a bipedal mode of locomotion for travelling long distances at speed (Forster, 1990). The absence of any manus impressions associated with *Gypsichnites* footprints supports Forster's interpretation of a habitual biped, whether or not the trace-maker was indeed *Tenontosaurus*. The foot skeleton of *Tenontosaurus* carries four well-

developed digits (Figure 4.6.2), though it is thought by some that digit I was not long enough to normally contact the ground (Forster, 1990).

Superorder Dinosauria Owen, 1842

Order Saurischia Seeley, 1887

Suborder Theropoda Marsh, 1881

Ichnogenus ***Irenichnites*** Sternberg, 1932

Original Diagnosis: "Functionally bipedal; tridactyl; digitigrade; digits well spread, not bound together by pad, and of uniform breadth throughout; claws blunt; digit II cut away from the rest of foot; phalangeal pads faintly shown; heel impression not complete; tracks small; stride relatively long; trackway narrow." (Sternberg, 1932, pp. 67)

Type Species: Irenichnites gracilis Sternberg 1932. Gething Formation (Early Cretaceous: Aptian) eastern British Columbia.

Irenichnites gracilis Sternberg, 1932

(Figures 4.7.1-3 and 4.8.1-4; Table 5)

Original Diagnosis: "The heel pad is not completely developed; the impression of digit II is separate from that of the rest of the foot; the toes are of uniform breadth and terminate in blunt claws. The tracks are relatively short and broad. One shows faint impressions of phalangeal pads in digits III and IV...The tracks are approximately in a direct line, and the stride is relatively long...This would suggest a very long-legged animal. All digits terminate in blunt claws, which are not deeply impressed.

The divarication varies somewhat, but in the central track of the series, which shows the best detail, the divarication of digits II and III is 38 degrees, of III and IV, 40 degrees." (Sternberg 1932, p. 68).

Emended Diagnosis: An ichnospecies of *Irenichnites* in which the digital pads and claws are well-impressed in some specimens. Digit II has two phalangeal pads and a

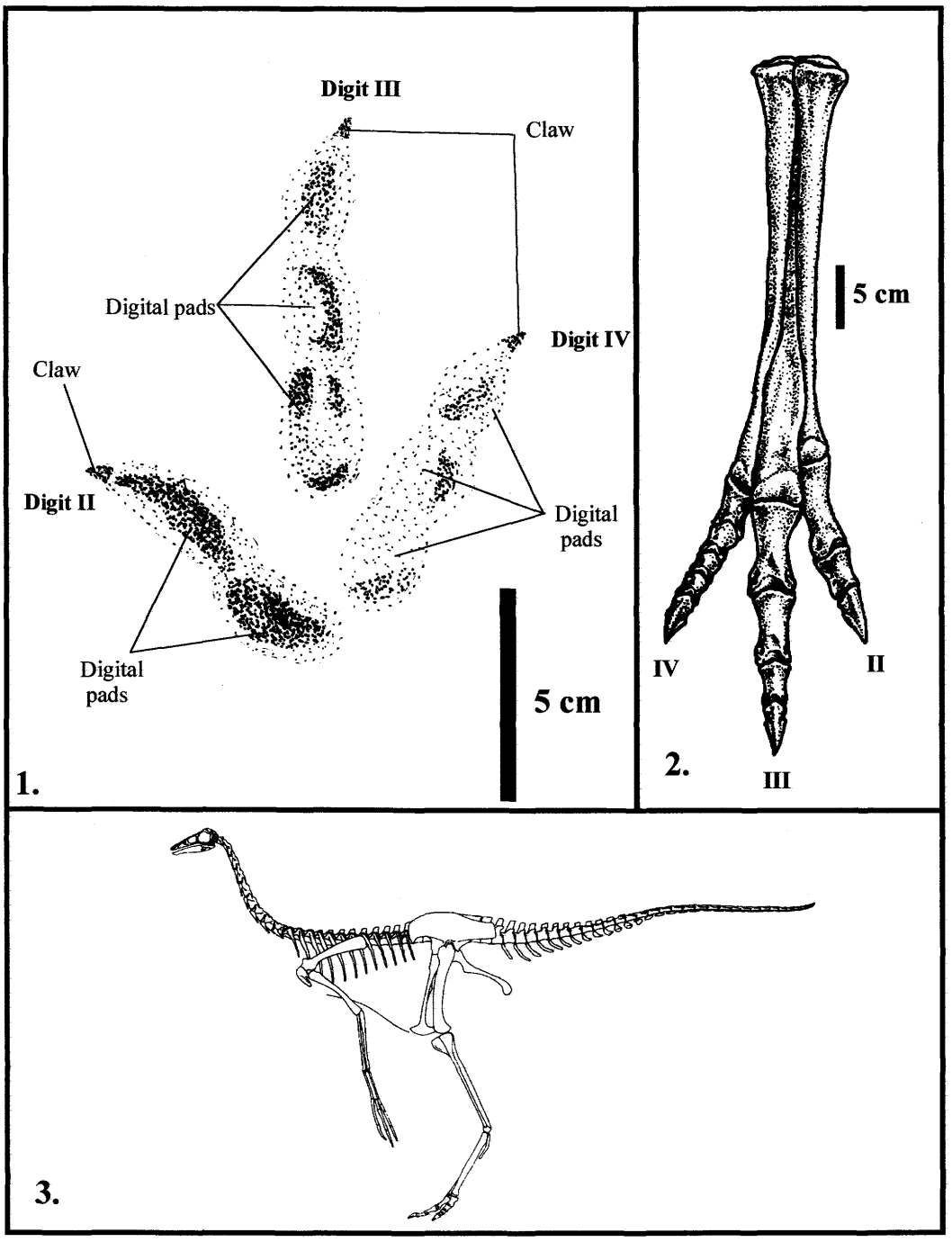

Figure 4.7.1-3: Morphology of *Irenichnites gracilis* footprint (Sternberg, 1932) compared to an ornithomimid foot. 1, Illustration of *Irenichnites gracilis* footprint (right pes) based on a replica cast (TMP 98.97.7) from Grid squares L/K7 (Figure 5.3). 2, Illustration of an ornithomimid (*Struthiomimus*) foot (reversed left pes) modified from Barsbold and Osmólska (1990). 3, Skeletal illustration of the ornithomimid, *Dromiceiomimus* (from Barsbold and Osmólska, 1990) whose foot skeleton compares closely in length to *Irenichntes gracilis* footprints.

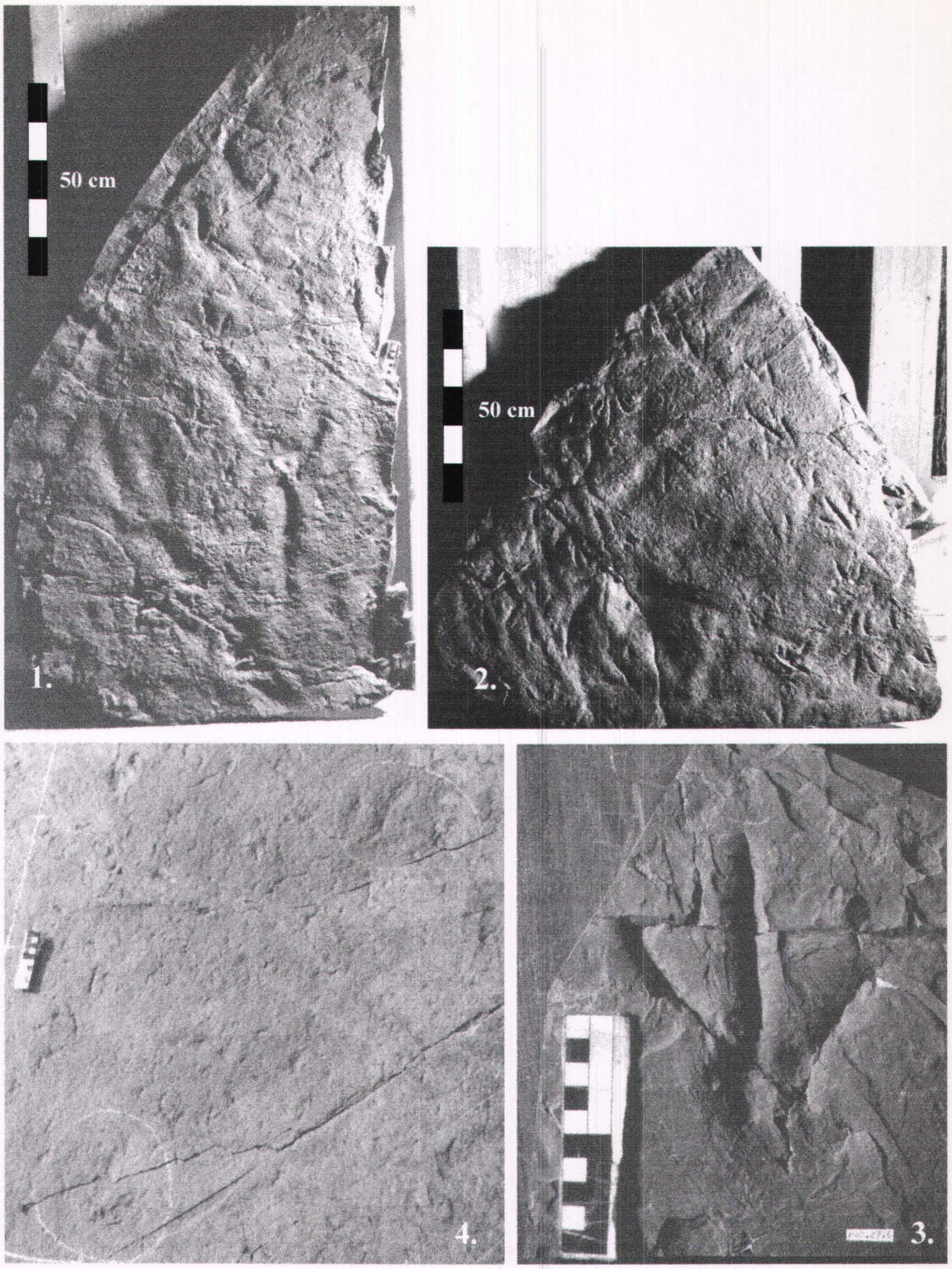

Figure 4.8.1-4: *Irenichnites gracilis* Sternberg, 1932; 1, Replica cast (TMP 90.27.3) of trackslab from the South Pit Lake site. 2, Replica cast (TMP 90.27.2) of trackslab from the South Pit Lake site. 3, Isolated left pes (TMP 90.27.6) from South Pit Lake site. 4, Faint pes prints *in situ* at the W3 Main site (Grid A21).

terminal claw; digit III has three phalangeal pads and a terminal claw; digit IV has at least three phalangeal pads and a triangular, terminal claw (Figure 4.7.1). Digits are of uniform breadth. Footprints are generally longer than wide (Table 5). The average footprint length/width ratio is 1.19, but varies considerably (1.1-1.31). These ratios are higher than those calculated from Sternberg's holotype (1932) which had a footprint length/width ratio of 0.90. Total divarication is low; between 60° and 80°. Pace and stride lengths (Table 5) indicate a long-legged animal. The trackway is very narrow, with the footprints positioned in almost a straight line with little or no rotation from the midline.

Materials: Specimens from the W3 Main tracksite and many from the South Pit Lake Site (Figure 4.8.1-4).

Description: See Sternberg (1932, p. 68) for detailed account.

Holotype: NMC 8552 (5 footprints: original natural moulds) lodged at the Canadian Museum of Nature, Ottawa, Ontario (Currie 1978, unpublished field notes).

Dimensions: See Sternberg (1932, p. 68). *Range of Dimensions:* See Table 5.

Remarks: This ichnospecies is emended to include the presence of phalangeal pads which have been observed in some specimens.

Discussion: The footprints of this animal are small in comparison to the other non-avian tridactyl prints described herein but, as Sternberg (1932) observed, they do have a lengthy stride, indicating a long-legged animal (Table 5). Thulborn (1990) identifies ornithomimid dinosaurs as the *Irenichnites* trace-makers. This identification was based on the digit II impression always being separated from the rest of the footprint, indicating that digit II was attached higher up the foot than the other weight-bearing digits. This is an arrangement that is observable in ornithomimid skeletons (Figure 4.7.2). The phalangeal pattern of the footprints also accords well with the phalangeal formula for ornithomimid pes skeletons, which (observed from illustrations) is 2:3:4:5:0 (Barsbold and Osmólska, 1990). The ornithomimid that produced *Irenichnites*

footprints would have been about the size of *Dromeceiomimus* (Figure 4.7.3), whose length of the pes skeleton (Barsbold and Osmólska, 1990) falls within the range of *Irenichnites* footprints observed at Grande Cache and Peace River. *Dromeceiomimus* is an Upper Cretaceous ornithomimid (Barsbold and Osmólska, 1990), but Ostrom (1970) has recorded the presence of ornithomimid skeletal elements from the Cloverly Formation (Aptian-Albian) of Montana and Wyoming, tentatively assigned to another Upper Cretaceous ornithomimid species, *Ornithomimus velox*. Similar ornithomimid skeletal elements are also found in other contemporaneous strata in the United States (Weishampel, 1990).

Superorder Dinosauria Owen, 1842

Order Ornithischia Seeley, 1887

Suborder Thyreophora Nopcsa, 1915

Ichnofamily Tetrapodosauridae Sternberg, 1932

Original Diagnosis: "Habitually quadrupedal; medium sized; bluntly pointed hoofs; trackway wide; stride short; no caudal impression. Tracks of this family were doubtlessly made by quadrupedal, predentate dinosaurs." (Sternberg 1932, p. 31)

Ichnogenus ***Tetrapodosaurus*** Sternberg, 1932

Original Diagnosis: "Quadrupedal; toes enclosed in pad or web; manus impressions in front of and completely separated from those of the pes; manus short and broad, five toes, digitigrade; pes of medium length, semiplantigrade, with four toes." (Sternberg 1932, p. 74).

Emended Diagnosis: Footprints of a medium-large quadrupedal animal; manual and pedal digits are not enclosed in a pad or web; footprints that appear to have this morphology are likely the result of deformation of the substrate caused by the weight of the animal. The degree to which this occurs largely depends on the consistency and compo-

sition of the substrate. The manus is wider than long with a concave posterior margin. The manus is approximately two-thirds the size of the pes (McCrea *et al.*, in press, Appendix A). There are five manual digits. The pes is slightly longer than wide. There are four pedal digits.

Type Ichnospecies: Tetrapodosaurus borealis Sternberg 1932. Gething Formation (Early Cretaceous: Aptian), eastern British Columbia.

Materials: Numerous specimens from several localities in the Smoky River Coal Mine near Grande Cache, Alberta.

Remarks: The diagnosis of this ichnogenus is emended to take into account the lack of any pad or webbing enclosing the manual and pedal digits.

Tetrapodosaurus borealis Sternberg, 1932

(Figures 4.9.1-3 and 4.10.1-8; Tables 6a-c and 7)

Original Diagnosis: "The manus is ahead of and completely separated from the pes. It is very short and broad. There appear to be five toes, though in some of the tracks only three are well outlined, probably due to inequality in the length of the toes and the nature of the surface over which the animal walked. In the Upper Cretaceous Ceratopsia only the three inner toes bore hoofs, and digits IV and V probably did not appear beyond the sole pad. The outer toes of the animal that made these tracks may have been too short to make an impression if the weight were thrown on the inside of the foot. The toes were enclosed in a large pad, except for the distal extremity which was free. This pad seems to have enclosed only the digits, differing from that of the pes, in which a metatarsal pad formed the posterior portion of the track. The divarication of the toes is much greater in the manus than in the pes, that of the outer toes being more than 180 degrees. Divarication of digits I and II, 73 degrees; of II and III, 42 degrees; of III and IV, 33 degrees; of IV and V, 50 degrees.

The pes is longer than broad and much of the weight was borne by the metatarsal

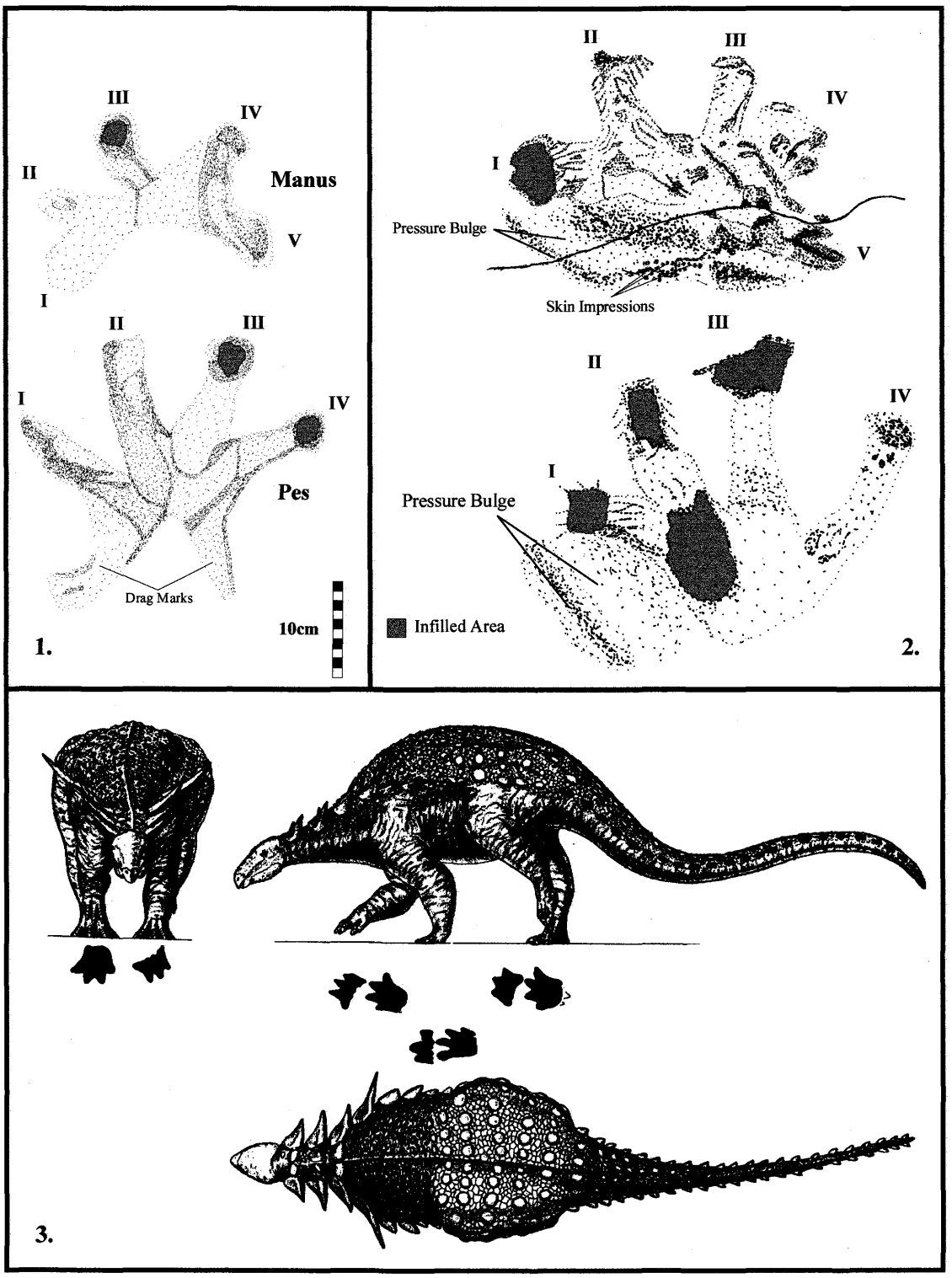

Figure 4.9. 1-3: *Tetrapodosaurus borealis* Sternberg, 1932; 1, Illustration of a right manus and pes (Grid B17/18),drawn from replica cast TMP 98.89.4. 2, Illustration of right manus and pes (Grid E/D10/11), drawn from replica cast TMP 98.89.2. 3, Life restoration of the nodosaurid ankylosaur, *Sauropelta* superimposed over Sternberg's illustration (1932) of *Tetrapodosaurus borealis* prints; modified from Carpenter (1984).

pads. All the phalangeal and metatarsal pads appear to have been fused into one mass. The toes extend only a short distance beyond the pad and terminate in small, rounded hoofs. The distal ends of most of the toes are slightly more deeply impressed than the sole of the foot. The posterior outline of the track is not well defined. There are four toes, and the outer one (?IV) is more divergent than the others. At the posterior edge of some of the tracks are triangular depressions, probably made by the dragging of the hoofs as the foot was coming to rest.

Divarication of digits I and II, 14 degrees, and II and III, 21 degrees, of III and IV, 32 degrees." (Sternberg 1932, p. 74).

Emended Diagnosis: A species of *Tetrapodosaurus* whose manual prints generally show the impression of five digits although some less perfectly preserved prints may show fewer digits. All five digits may be visible; they are not completely enclosed in a large fleshy pad. The digits join proximally in a relatively small manual pad. The inner digits (II-IV) generally face forward while the outer digits (I and V) are directed laterally (Figure 4.9.2) or even posteriorally (Figure 4.9.1). Digit I is long and slender, often positioned nearly perpendicular to the mid-line of the trackway. The features of digit I are very useful in identifying whether isolated manus prints are left or right. The divarication of the manus prints is variable, but often quite high, from 100° to over 200° (Table 6c; Figure 4.9.1-2).

The digits of the pes are quite elongate and slender; they are not enclosed in a fleshy pad (Figure 4.9.1-2). Digit I is short and is positioned medially on the foot while digits II-IV are longer and positioned anteriorly. Even in poorly preserved pes footprints and natural casts, this arrangement of the digits can assist in determining if prints are left or right. The divarication of the pes digits is much lower than that of the manus, between 70° and 80° (Table 6a and c). The toes are more deeply impressed than the rest of the foot. Posterior drag marks may be present; they are triangular.

Description: See Sternberg (1932, p. 74) for detailed account.

Holotype: NMC 8556 (6 footprints: 3 manus, 3 pes; replica cast: cast and mould) lodged at the Canadian Museum of Nature, Ottawa, Ontario (Currie 1978, unpublished field notes).

Dimensions: See Sternberg (1932, p. 74). *Range of Dimensions:* See Tables 6a-7.

Remarks: This ichnospecies is emended to include observations on the slender nature of the manual and pedal digits, their relative positions and further divarication measurements.

Discussion: Many *Tetrapodosaurus* footprints found at the several Grande Cache tracksites are similar in morphology to those that Sternberg (1932) originally described. However, there is also a wider spectrum of morphological variation seen in the thousands of *Tetrapodosaurus* footprints from the Gates Formation (Figure 4.10.1-8), similar to the situation (previously mentioned) that Gatesy *et al.,* (1999) encountered with *Grallator* footprints. The variations do not warrant the description of new ichnotaxa; rather they provide the opportunity to observe, at one site, the amount of variation that is possible in footprint preservation within an ichnotaxa on variable substrate conditions, since many of these preservation variations occur together on the same Bedding-plane, even though produced by animals of similar size pursuing similar activities (Bromley, 1990). For example, deeply impressed prints with prominent mud bulges and poorly defined digital impressions have been observed alongside footprints that are much more shallowly impressed with very well-defined digits, but which were made by a similar sized animal. The only explanation for this is that the deep, mud-bulged prints were made when the substrate had a high water content (i.e. muddy) while the shallow, well-defined prints were made after the substrate had de-watered and firmed up (i.e. time had elapsed).

A short summary of the observed morphological variation of *Tetrapodosaurus* prints from the W3 Main footwall is in order:

Morphotype A: Sequences of shallow, oval-shaped depressions with manus and

pes almost indistinguishable (Figure 4.10.1). Each oval depression contains the manual and pedal impressions. This morphotype was likely produced on a cohesive substrate that deformed plastically when the trace-producing animal traversed it. The bedding-plane below must have been saturated with water and, when pressure was applied during each footfall, the sediment of the underlying bedding-plane was deformed, allowing the overlying substrate that it was supporting to sag. There are a several underprints on the B-layer (Figure 5.3) that underlies the A-layer, which was the original footprint surface where this morphotype has been observed, This suggests that the underlying layer had a high water content when the prints were formed.

Morphotype B: Heavily impressed manus and pes prints with well-developed mud bulges (Figure 4.10.2). Difficulty in distinguishing individual digits, but the position of the manus and pes are clearly visible.

Morphotype C: Moderately impressed manus and pes, associated with mud bulges (Figure 4.10.3). Only the distal portions of the digits are separate from the manus and pes (giving the impression of webbing). The substrate still had a substantial amount of water content for the trace-maker to produce the mud bulges.

Morphotype D: Mud bulges formed mostly on the inside portions of the footprints (Figure 4.9.2). The outline of the digits is much more clearly defined (no "webbing"). Skin impressions may be present.

Morphotype E: Lightly impressed manus and pes, but with sharp outline of lengthy digits (Figure 4.9.1 and 4.10.4-6). Posterior outline of some pes digits may be visible within the print (Figure 4.9.1). These prints appear to reflect the true arrangement of skin and bone more accurately.

Morphotype F: Outline of prints, very faint. Major feature is presence of depressions representing the tips of the manus (5) and pes (4) digits. The substrate had dried and consolidated to the point where even a heavy, *Tetrapodosaurus* footprint producing animal left little trace other than the tips of its digits. This conforms to

Thulborn and Wade's (1989) "kick-off phase" of the step cycle, where only the tips of the digits break through the substrate.

Sternberg (1932) originally identified ceratopsians (an Upper Cretaceous group) as the producers of *Tetrapodosaurus* prints. However, Carpenter (1984) convincingly matched footprints of *Tetrapodosaurus* to *Sauropelta*, a genus of nodosaurid ankylosaur from the Cloverly Formation which is contemporaneous with this footprint site (Figure 4.9.3). While *Tetrapodosaurus* footprints could have been produced by *Sauropelta*, footprints produced by other nodosaurid and ankylosaurid genera (with five manus digits and four pes digits) would be very similar, and would likely be classified as the same ichnospecies. Some ceratopsians also have a pentadactyl manus and a tetradactyl pes, capable of producing this type of footprint (hence Sternberg's original assignment). Even though large ceratopsians are primarily found in the Campanian and Maastrichtian of the Upper Cretaceous (Dodson, 1996), recent discoveries of early Upper Cretaceous large ceratopsians in the Turonian (Wolfe and Kirkland, 1998) have been documented. McCrea *et al.*, (in press, Appendix A) compare skeletal and footprint morphology and biostratigraphy in order to differentiate the footprints of the ankylosaurs from those of ceratopsians. Based upon the criteria established (McCrea *et al.*, in press, Appendix A), *Tetrapodosaurus* prints were most likely made by ankylosaurs.

Class Aves

Morphofamily Avipedidae Sarjeant and Langston, 1994

Ichnogenus ***Aquatilavipes*** Currie, 1981

Original Diagnosis: "Made by a bipedal animal with three functional digits. Width greater than length; average divarication of digits II and IV greater than 100°. Digit IV longer than digit II and shorter than digit III. Sharp claw on each digit. No hallux impression" (Currie 1981, p. 259).

Emended Diagnosis: Footprints of small to large size, showing three digits

united proximally, most often in a metatarsal pad ("heel"); webbing and hallux lacking. Digits slim, their maximum width less than 15% of their length; digit III is more than 25% longer than the medial digits. Total interdigital span greater than 95° and often exceeds 120°. Length of digits II and IV may be similar, but digit IV is frequently somewhat longer. All digits clawed, the claws frequently showing inward flexure in relation to the digit axis. Digital pad impressions may be visible on better-preserved molds or casts — three to four on digit III, two on digits II and IV.

Type Ichnospecies: *Aquatilavipes swiboldae* Currie, 1981. Gething Formation (Early Cretaceous: Aptian), eastern British Columbia.

Remarks: The ichnogeneric diagnosis is here emended to clarify differences from *Fuscinapeda* Sarjeant and Langston, 1994. (The diagnosis of the latter ichnogenus is emended below). An earlier emendation by Lockley *et al.*, (1992, p. 125), which added to Currie's diagnosis a mention of "faint digital pad impressions," is incorporated, even though their presence or absence depends upon the substrate. As emended here, *Aquatilavipes* differs from *Fuscinapeda* essentially in having more slender digits and from *Aviadactyla* Kordos, 1983, in the proximal fusion of the digits and their less "stick-like" character. It differs from the otherwise very similar *Ludicharadripodiscus* Ellenberger, 1980, in the consistent lack of a hallux impression. The digit impressions of *Avipeda* Vialov, 1965, emend. Sarjeant and Langston, 1994, are shorter and thicker (see also Vialov, 1966); those of *Ornithotarnocia* Kordos, 1983, show a thicker digit III and a higher degree of asymmetry.

Aquatilavipes swiboldae Currie, 1981

Figure 4.11.1-2: Table 8 (TMP 79.23.3 and BCPM 744)

1981 *Aquatilavipes swiboldae* Currie, p. 259-261, figs. 1a, c, 2, 3.

1992 *A. swiboldae* Currie emend. Lockley *et al.*, p. 115-116, 125, 129, fig. 4.

1994 *A. swiboldae* Currie. Sarjeant and Langston, p. 12.

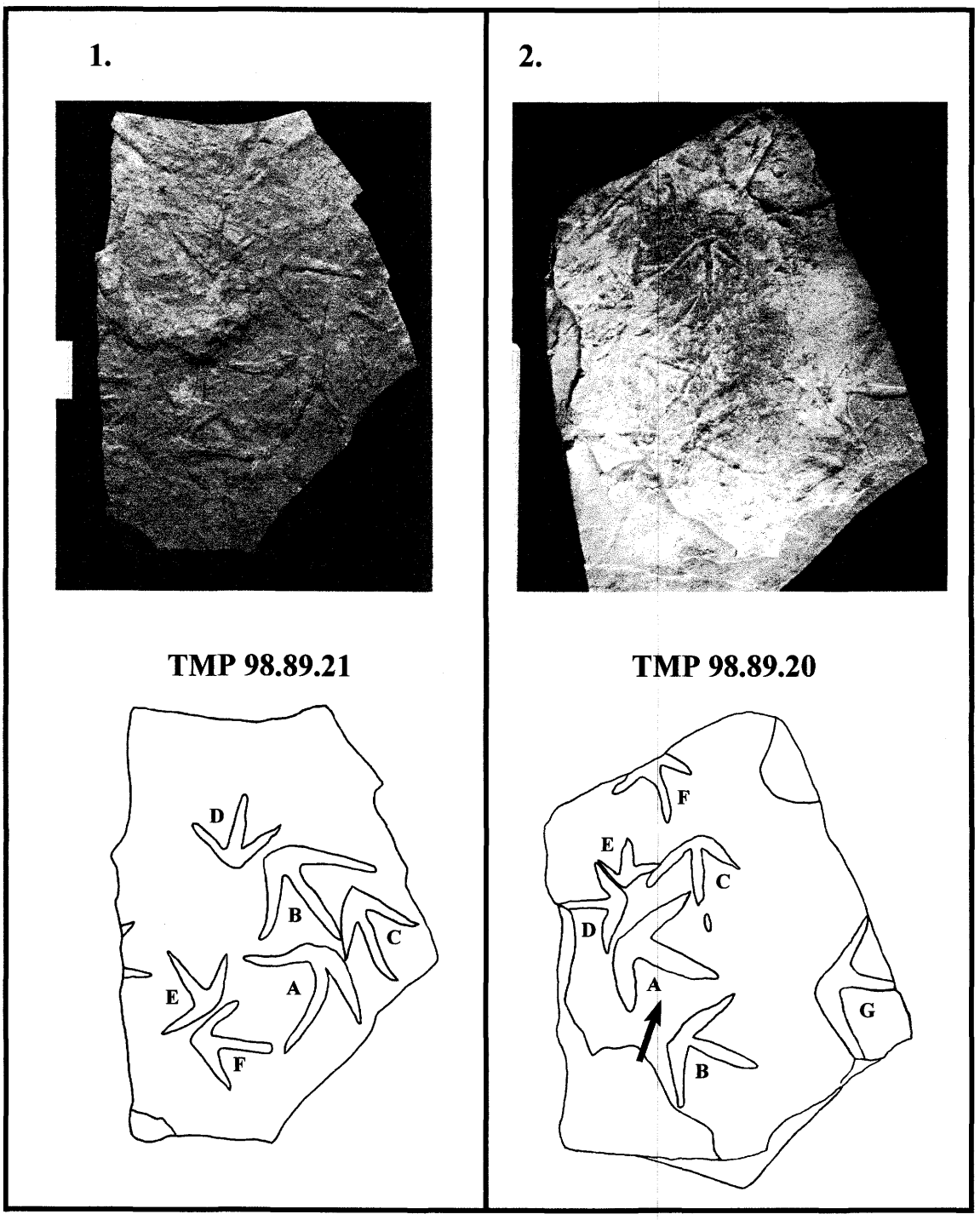

Figure 4.11.1-2: 1 Photograph and illustration of natural casts of *Aquatilavipes swiboldae* prints (TMP 98.89.21) from the W3 Bird site. 2, Photograph and illustration of natural moulds of *Aquatilavipes swiboldae* prints (TMP 98.89.20). Note: The line drawings represent the position of the prints on the slabs and are not intended to be indicative of the morphological detail of these specimens.

Original Ichnospecies Diagnosis: "Footprints less than 4.5 cm in length, average width 26% greater than length: average divarication of digits II and IV is 113°. Digit III about 50% longer than digit II and 40% longer than digit IV" (Currie, 1981, p. 259).

Emended Ichnospecies diagnosis: A species of *Aquatilavipes* of small size, with slim digits; the thickness of the slimmest digit (III) is less than 8% of its length, the others being somewhat thicker (up to 12.5% of length). All digits terminate in claws, that on digit III being especially acute. The digits were flexible, digits II and III generally curving inwards distally, digit IV outward. Digit III is about 50% longer than digit II and 40% longer than digit IV. Total interdigital span varies from 90° to 130°, averaging 113°. The angle of the footprints to the center of the trackway (footprint rotation) varies, but they tend to be directed inward. The trackway is of moderate breadth.

Description: See Currie (1981, pp. 259-261) for detailed account.

Holotype: Footprint no. 76 (mould and cast). Mould (specimen TMP 79.23.37) lodged in the Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta: cast (specimen BCPM 744) lodged in the Royal British Columbia Provincial Museum, Victoria.

Dimensions: See Currie (1981, p. 259-260) for details.

Remarks: The diagnosis is here amplified to facilitate comparisons with *A.* ichnosp. nov. All features of the original diagnosis are included. The dimensions of the specimens from Grande Cache are shown in Table 8; these differ from Currie's in that they were taken to the back of the metatarsal pad.

Aquatilavipes ichnosp. nov.

(Figures 4.12-14; Table 9a and b)

Ichnospecies Diagnosis: A species of *Aquatilavipes* of moderately large size, the thickness of the digits being around 10% of their length. The digits terminate in narrow, sharp claws, those of digits II and IV inclined slightly inward towards digit III. Total interdigital span varies between 120° and 135° according to gait and substrate hardness,

the angle between digits II and III being consistently larger than between digits III and IV.

Digital pads often discernible — three on digit III, two on digits II and IV. The center of each digit impression may show a groove parallel to the axis of the digit, continuous or discontinuous; this may not be evident in shallower imprints. The angle of the footprints is always slightly inward towards the center of the trackway; the trackway is quite broad and the pace, though variable, consistently short.

Holotype: Specimen no. TMP 98.89.11; cast of isolated left pes taken from Grid H/G16 (Figure 4.12). Lodged in the Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta.

Paratype: Specimen no. TMP 98.89.10; cast of trackways (Figures 4.13 and 4.14). Same lodgement.

Horizon and Locality: Grande Cache Member of the Gates Formation, early Albian (Lower Cretaceous), Smoky River Coal Mine (Smoky River Coal Limited) about 21 km northwest of Grande Cache, Alberta. Located on the footwall of the W3 Main site below the No. 4 coal seam.

Dimensions: Holotype (by standard measurement): overall length 7.9 mm, overall breadth 9.5 mm; length of

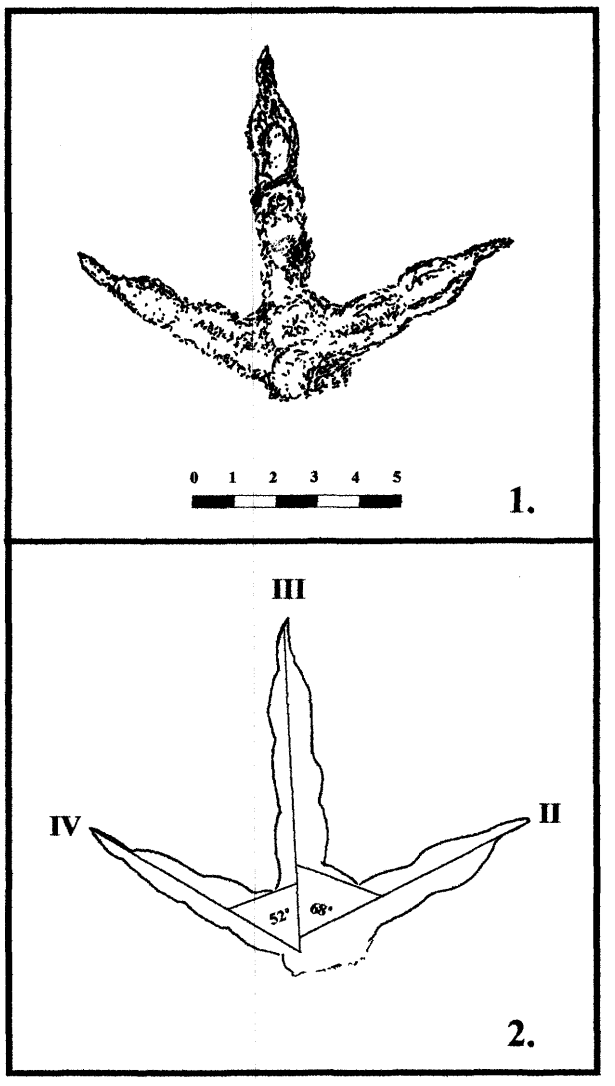

Figure 4.12. 1-2: 1, *Aquatilavipes* ichnosp. nov. holotype drawn from replica cast TMP 98.89.3; illustrated in Figure 5.3 (Grid H/G16). 2, Divarication of digits (Figures illustrated by Dr. W.A.S. Sarjeant).

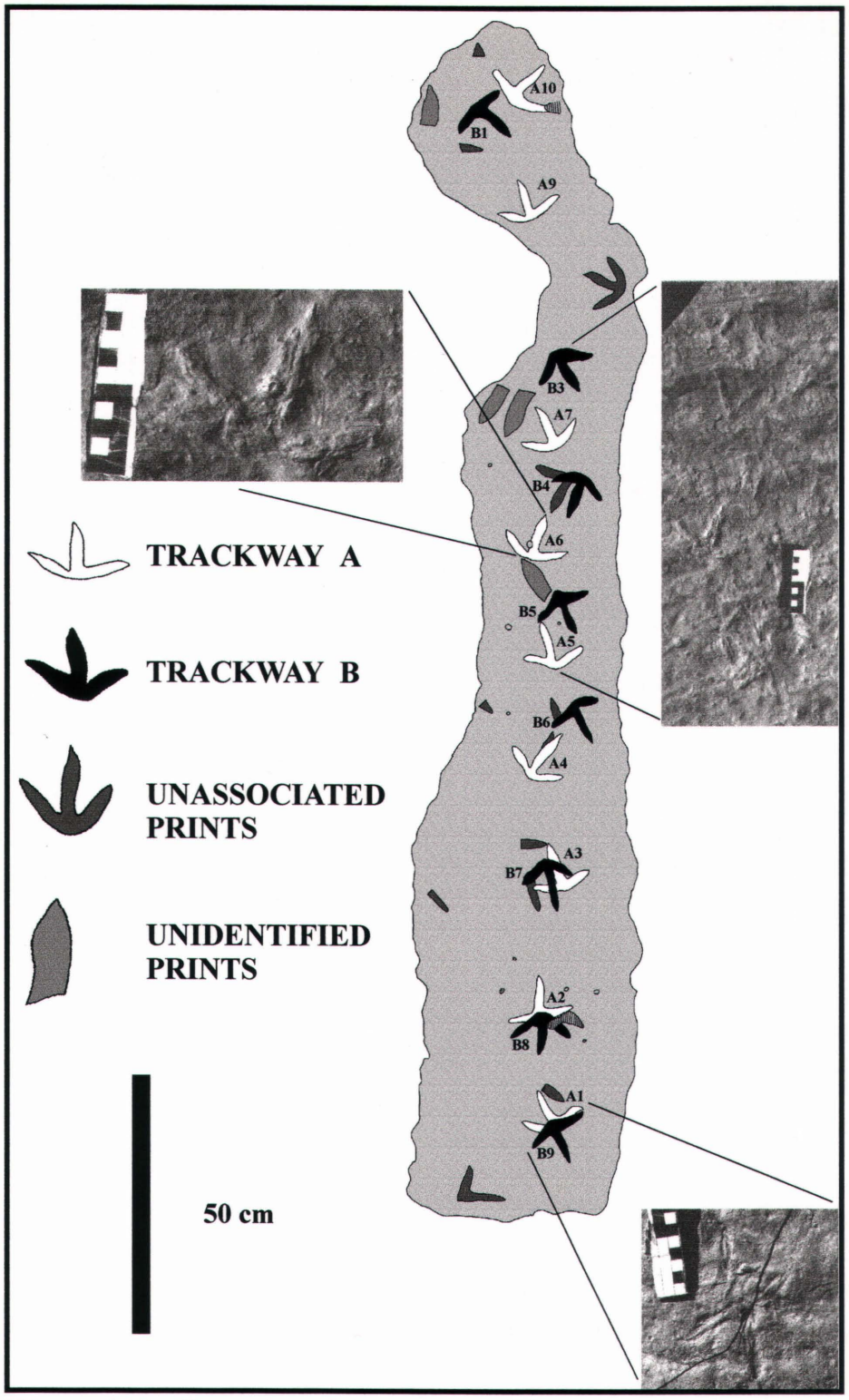

Figure 4.13. Illustration of *Aquatilavipes* ichnosp. nov. trackways (A and B) and *A.* indet. footprints above the main research area (Figure 5.2.1-2) on the W3 Main Site (based on a replica cast TMP 98.89.10). Photographs of trackways and prints were taken of original specimens on the W3 Footwall.

digits II, 4.5 mm: III, 6.7 mm: IV, 5.0 mm. *Paratype*: Table 9b. *Range of dimensions*: See Tables 9a and 9b. *Interdigital Angles*: Holotype: see Figure 4.12.2. Range: see diagnosis.

Remarks: The footprints are present on at least three bedding-planes on the W3 footwall (W3 Main tracksite). They are found in association with numerous dinosaur footprints. Ten trackways and over 750 individual footprints of this ichnospecies were studied.

The paratype slab (Figure 4.13) shows that two birds were moving at moderate speed in opposite directions, with a moderately long stride and broad trackways (11.5 -

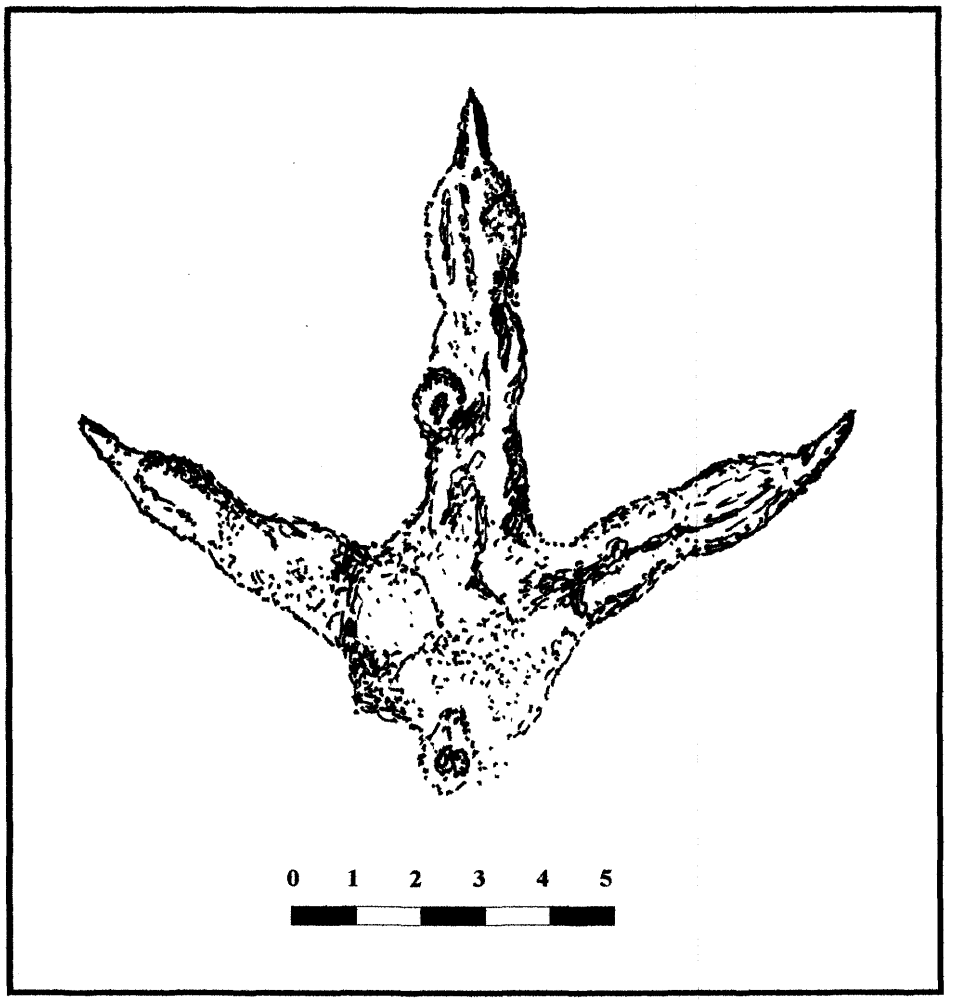

Figure 4.14. Illustration of *Aquatilavipes* ichnosp. nov. footprint A6 (Figure 4.13) showing an apparent deformity. Figure drawn by Dr. W.A.S. Sarjeant.

14 cm). One print, number A6 on the paratype trackway (Figure 4.13 and 4.14) shows crater-like swellings, at left on digit III and at right on the metatarsal pad. These are comparable to the pathological effects produced by bumblefoot in living poultry (Dr. Peter Flood, pers. comm., 1999) but it is perhaps more likely that they result from the activity of infauna in the sediment. Unfortunately, the other prints of this foot in the trackway were not good enough to distinguish between these alternatives.

Ichnogenus ***Fuscinapeda*** Sarjeant and Langston, 1994

1994. *Fuscinapeda* Sarjeant and Langston, p. 13-14.

Original Diagnosis: "Avian footprints of small to large size, showing three digits, slim or moderately thick (II to IV). Digit III is characteristically more than 25% longer than the lateral digits. Total interdigital span greater than 95° and often exceeds 110°. Digits united proximally, frequently showing a distinct "heel." Webbing absent or restricted to the most proximal part of the interdigital angles" (Sarjeant and Langston, 1994, p.13).

Emended Diagnosis: Tridactyl footprints of small to large size, showing three digits united proximally, most often in a metatarsal pad ("heel"); webbing and hallux lacking. Digits moderately thick to thick, their maximum width exceeding 15% of their length: digit III is more than 25% longer than the lateral digits. Total interdigital span greater than 95° and often exceeds 120°. Length of digits II and III may be similar, but digit IV is frequently somewhat larger. All digits clawed, the claw frequently showing inward flexure in relation to the digit axis. Digital pad impressions are visible on better-preserved moulds or casts — three or four on digit III, two on digits II and IV.

Type Ichnospecies: *Fuscinapeda sirin* (Vialov, 1966) Sarjeant and Langston 1994. Miocene (Helvetian), Ukraine.

Remarks: The diagnosis of this avian ichnogenus is emended to clarify that it differs from *Aquatilavipes* in the greater thickness of the digits.

Avian Footprints, ichnogen. indet.

Figure 4.13 (upper left)

Large, incomplete bird footprints occur on the second of the three bird footprint-bearing layers (layer B). Two impressions of single digits and one imprint exhibiting two unconnected digits may be seen on the paratype slab (Figure 4.13, while two imprints showing two connected digits were seen on another area on the W3 footwall (Figure 5.3, Grid H19), but no complete prints have yet been discovered. The nature and relative orientation of the digits are similar to those of *A.* ichnosp. nov., but represent footprints of a much larger bird, the length and width of the digits indicating that a complete print could be from one-and-a-half to three times the size of *A.* ichnosp. nov. prints (approximately 14-18 cm in length). These dimensions approach those of *Magnoavipes lowei* from the Cenomanian of Texas (Lee, 1997), and *Archaeornithipus meijidei* from the Berriasian of Spain (Fuentes Vidarte, 1996). The digits of the large bird prints from Grande Cache are much thicker than the slender digits of *Magnoavipes* and *Archaeornithipus*; however, *Magnoavipes* and *A.* ichnosp. nov. resemble one another in not showing any trace of a hallux impression. Because of the unsatisfactory character of the material discovered so far, it is not appropriate to describe what may become a new ichnotaxon.

Discussion: Although purported bird footprints were discovered in the Upper Cretaceous (Cenomanian) Dunvegan Formation along the Pouce Coupe River, Alberta, by C.R. Stelck in 1951 (Currie, 1989), no formal descriptions of these prints (UALVP 25271) have yet been published. It is questionable whether they are truly avian. The first published record of bird footprints in Cretaceous strata of western Canada was from the Gething Formation (Aptian) of the Peace River Canyon in eastern British Columbia (Currie, 1981). Lockley and Rainforth (in press) report five bird tracksites in western Canada. With the addition of the bird tracksite described herein, at least six are now known. In ascending stratigraphic order, these are:

Aquatilavipes swiboldae, Gething Formation (Aptian), Peace River Canyon, northeastern British Columbia (Currie, 1981); *A. swiboldae*, Gladstone Formation (Aptian) near Grande Cache, western Alberta (Lockley *et al.*, 1992); *A.* ichnosp. nov. , *A. swiboldae* and ichnogen. indet., Gates Formation (Albian) near Grande Cache, western Alberta (herein); *Jindongornipes*-like bird prints, Dunvegan Formation, British Columbia (Lockley and Rainforth, in press); ichnosp. indet., St. Mary's River Formation, (Maastrichtian), southern Alberta (Lockley and Rainforth, in press) and ichnosp. indet., Horseshoe Canyon Formation (Maastrichtian), eastern Alberta (Lockley and Rainforth, in press).

The *A. swiboldae* trackways discovered in the Peace River Canyon were neither directly associated with dinosaur footprints (Currie, 1981), though these are present elsewhere in the canyon (Sternberg, 1932), nor have dinosaur or bird bones been discovered in adjacent strata. At the W3 Main tracksite, the original discoveries were made in talus blocks; the *A. swiboldae* footprints seen in the outcrop were not associated with dinosaur footprints.

In contrast, the *Aquatilavipes* ichnosp. nov. trackways occur in association with an abundance of dinosaur footprints — of *Tetrapodosaurus* (ankylosaurs) as well as *Irenesauripus*, *Columbosauripus*, *Gypsichnites* and *Irenichnites*: a rich late Lower Cretaceous fauna (McCrea and Sarjeant, 1999; McCrea *et al.*, in press, Appendix A). They are preserved in a rippled sandstone surface that contains an abundance of large and small invertebrate traces.

The *A.* ichnosp. nov. footprints are those of large wading birds, possibly in quest of invertebrate food; however, no dabbling marks from the beaks of the birds were recognized. Since there are no mud cracks, it is likely that the footprints were either made under a water cover a few centimeters deep or that the sediments, though exposed to the air, were so water-saturated that they did not dry out completely before burial by later sediments.

On the paratype slab (Figure 4.13), the prints from Trackway A are better defined than those of Trackway B, even though the Trackway B prints overlie those of Trackway A. Evidently, an interval of time elapsed between the formation of the two trackways, during which the substrate became slightly more cohesive.

Bird or dinosaur?: Footprint length and width measurements of all bipedal ichnotaxa that occur on the W3 Main footwall within the study area (McCrea and Sarjeant, 1999) were compared using footprint length/width ratios (Figure 4.15.1-3). This method of measurement was used initially to attempt to distinguish the footprints produced by theropods from those of ornithopods, following the procedure of Moratalla *et al.*, (1988). The footprint length/width ratios of the bipedal dinosaur ichnotaxa from W3 Main site are as follows: *Irenesauripus mclearni* (1.20, N=10), *Columbosauripus ungulatus* (1.09, N=12), *Irenichnites gracilis* (1.19, N=11) *and Gypsichnites pascensis* (1.19, N=27). As discussed previously, average footprint length/width ratios for all the dinosaur ichnotaxa are less than the 1.25 ratio used by Moratalla *et al.*, (1988) to distinguish footprints of ornithopods and theropods (theropod >1.25>ornithopod). However, the presumed avian prints of *Aquatilavipes* ichnosp. nov. have a much lower average ratio, (0.73, N=47), which is distinct from dinosaurian ichnotaxa ratios (Figure 4.15).

Currie's (1981) calculation of average footprint length and width for *A. swiboldae* prints produces a ratio (FW/FL) of 0.80 (N=44) that is quite similar to that of *A.* ichnosp. nov. He also studied the footprints of some extant paludicolus birds - the killdeer (*Charadrius vociferus*) and the great blue heron (*Ardea herodias*) for comparison with *Aquatilavipes swiboldae* footprints. Using the original data from Currie's study, the calculations of their footprint length/width ratios are: *C. vociferus* (0.88, N=40), *A. herodias* (0.90, N=14). These values are slightly higher than those of *Aquatilavipes swiboldae* and *A.* ichnosp. nov., but still well below the average ratio of the W3 Main dinosaur ichnotaxa. By using footprint length/width ratios, as well as the criteria set out

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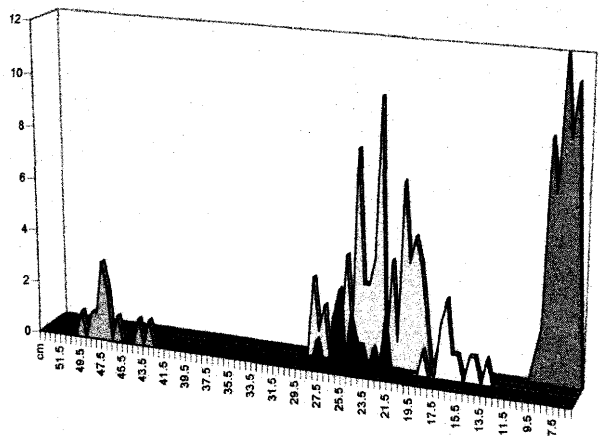

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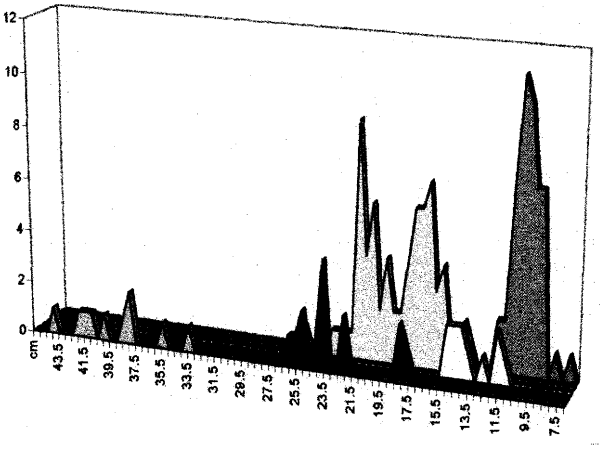

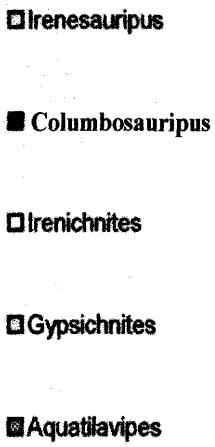

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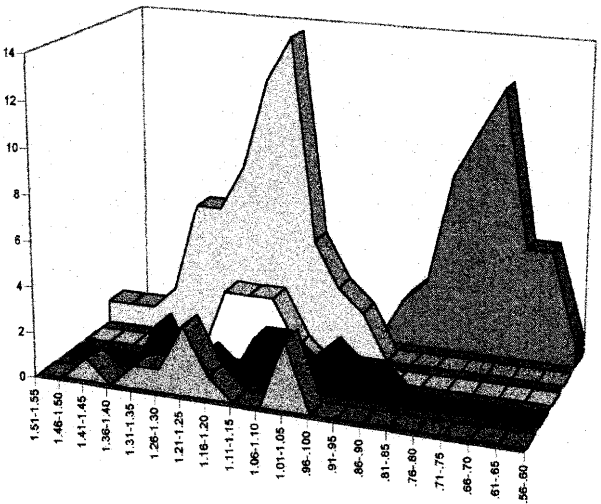


Figure 4.15. Comparisons of footprint measurements between tridactyl ichnotaxa. Data taken from Tables 1, 3-5 and 10. 1, Comparison of footprint length (FL) measurements (cm). 2, Comparison of footprint width (FW) measurements (cm). 3, Comparison of footprint length/width (FW/FL) ratios.

by Lockley *et al.*, (1992) it is possible to distinguish the footprints made by birds from those made by dinosaurs. Further research needs to be conducted in this area, particularly on the study of modern footprints produced by different taxa of extant birds.

Class Mammalia

Ichnogenus ***Tricorynopus*** Sarjeant and Langston, 1994

Tricorynopus? ichnosp. nov.

(Figures 4.16 and 4.17)

Diagnosis: Very small digitigrade to semidigitigrade, tridactyl footprints, the imprints of one foot (the presumed pes) being almost twice as large as those of the other foot (the presumed manus). In the presumed manus, the digits radiate symmetrically from the base, with an interdigital span of around 15°; they are moderately thick proximally and become narrower distally. All digits show sharp claws, directed more or less forward. The presumed pes had more flexible and widely-spread digits, with an interdigital span of around 60°. In both manus and pes, digit III is longest. In the presumed manus, digits II and IV are of similar length, whereas digit IV of the presumed pes is longer than digit III and curves outward. Trackway pattern not determined.

Holotype: Imprints at lower center of slab with *Aquatilavipes swiboldae* footprints (TMP 98.89.20), lodged in the Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta (Figures 4.16 and 4.17).

Dimensions: Holotype: presumed manus: length overall 3.5 mm, breadth 3.0 mm. Presumed pes: length overall 7.5 mm, maximum breadth 6.5 mm. Other imprints (Figures 16 [lower], 4.17.3) not capable of measurement.

Horizon and Locality: Holotype: Grande Cache Member of the Gates Formation, early Albian (Lower Cretaceous), Smoky River Coal Mine (Smoky River Coal Limited) about 21 km northwest of Grande Cache, Alberta. Discovered in the talus at the base of the W3 footwall.

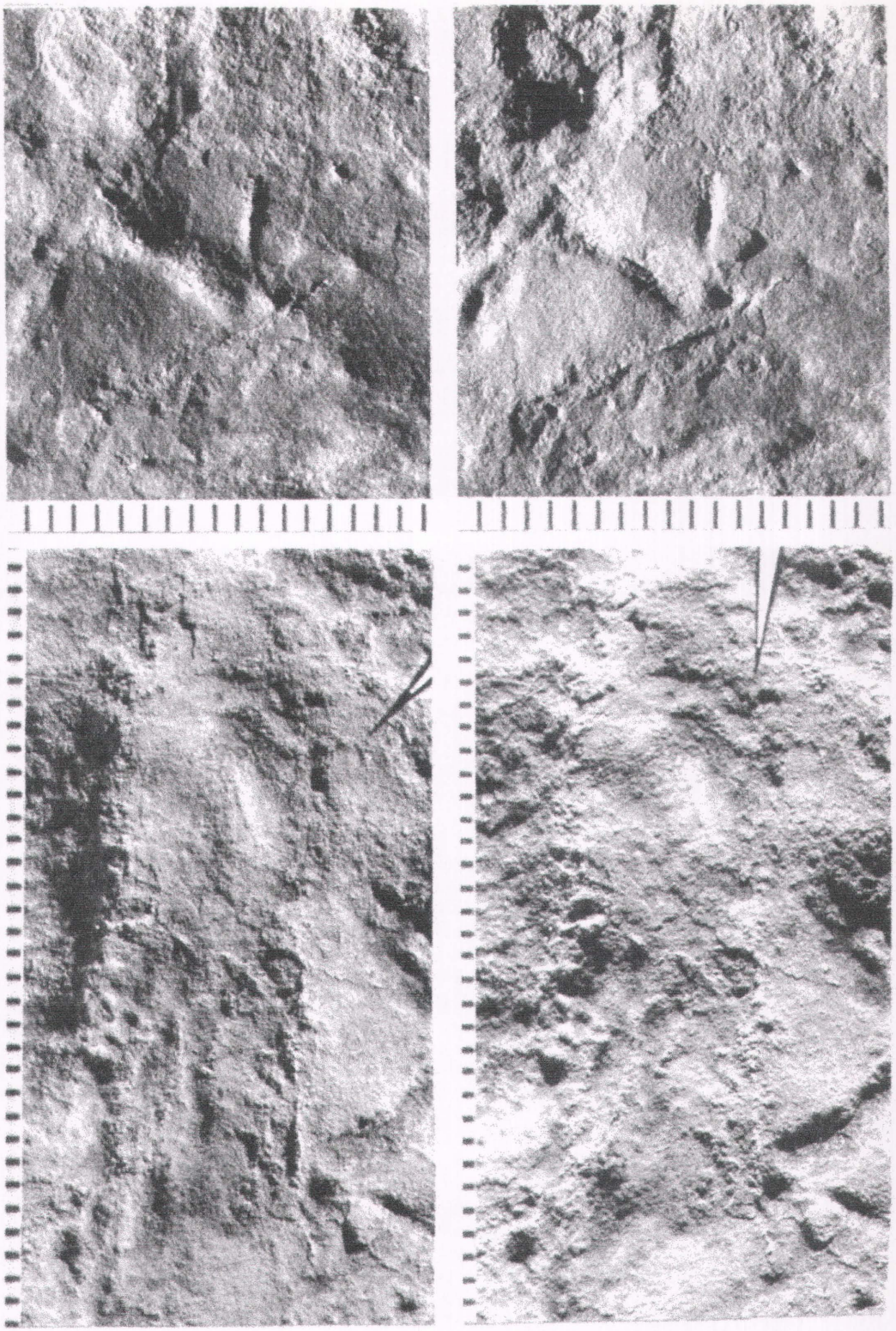


Figure 4.16. Photographs of *Tricorynopus?* ichnosp. nov. Upper left and right: the holotype impressions, in two directions of illumination. Lower left and right: other, less clearly impressed prints, in two directions of illumination (indicated by arrows).

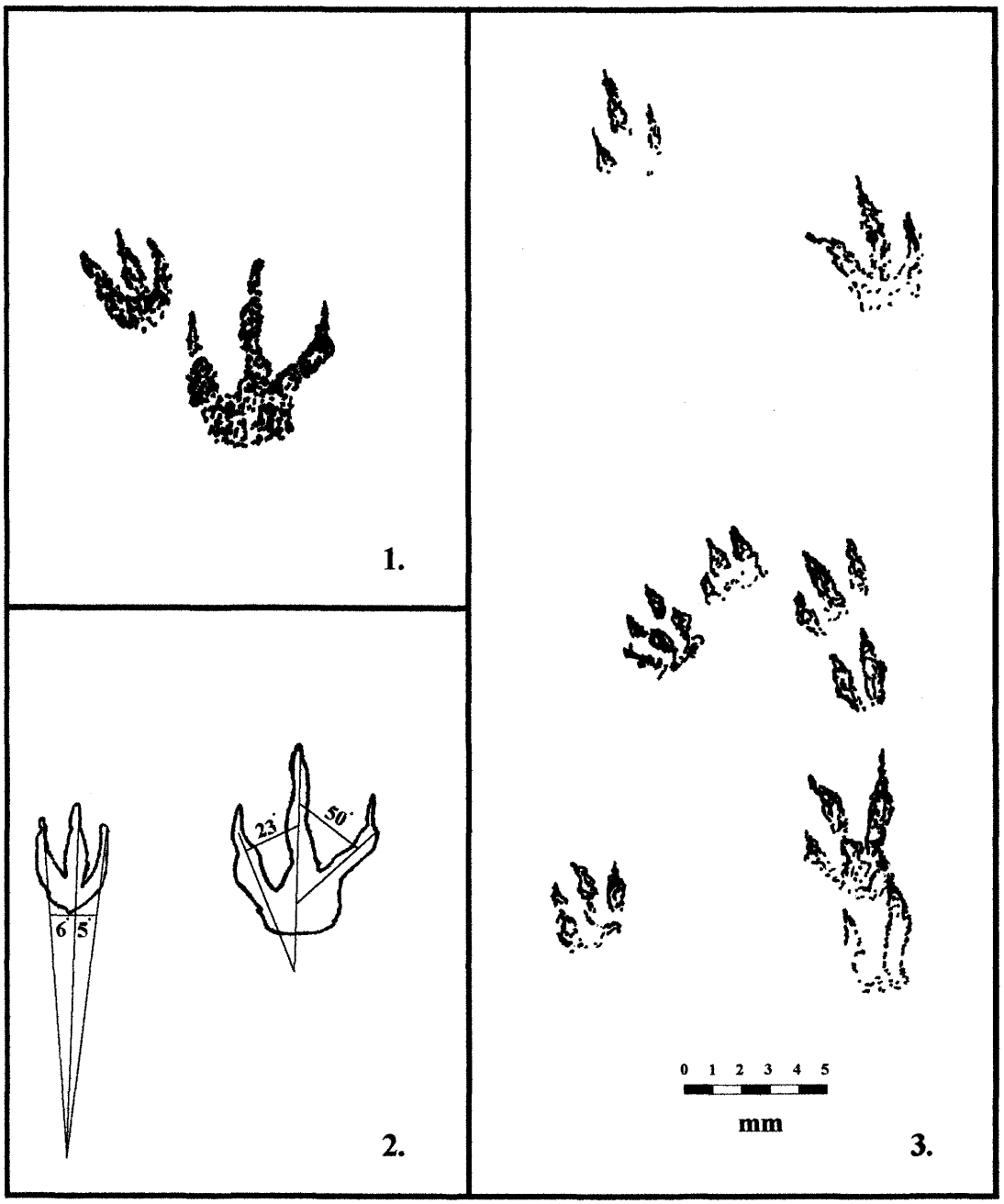


Figure 4.17.1-3: 1, *Tricorynopus?* ichnosp. nov.; sketch of the holotype print; left (and upper),presumed right manus; right (and lower), presumed right pes (corresponding to Figure 4.16, upper). 2, *Tricorynopus?* ichnosp. nov.; inter-digital angles. Left: presumed manus. Right: presumed pes. Note: measurements taken along the digit proper: all claws point forward. 3, *Tricorynopus?* ichnosp. nov.; Sketch of other mammalian prints on the slab (corresponding to Figure 4.16, lower). Note that a flaking-off surface has caused some prints to be incomplete at right. (Figures illustrated by Dr. W.A.S. Sarjeant).

Remarks: Though a number of these small mammalian footprints are present on the lower central region of the type slab, neither the gait nor any indication of superposition could be discerned. In consequence, the distinction between manus and pes is based wholly on the presumption that the latter is likely to be larger than the former — an assumption difficult to justify when so little is known about the post-cranial morphology of small mammals of the late Mesozoic. A problem was the very light weight of the track makers: animals so small — only a few tens of grams — inevitably make very shallow footprints. These footprints do not altogether accord with the diagnosis of the ichnogenus *Tricorynopus*, in that the presumed manus and presumed pes differ markedly in size. If the discovery of further specimens enables the trackway pattern and the identity of the manus and pes to be determined, it is likely that they will be placed into a new ichnogenus.

The lack of a determinable trackway and the extreme shallowness of the prints make it difficult to make detailed comparisons with any known group of mammals that might have made these footprints. Their size is not very diagnostic, since Lillegraven (1979) notes that Mesozoic mammals in general "...were in the size range of modern shrews to rats". It is because of the small size and frailty of their bones that only the teeth — not prone to digestive or erosional decay — are normally preserved.

In attempting a correlation between footprints and potential track makers, two methods of comparison are possible. The first is to compare the morphology of the footprint directly with known skeletal material. Since, in the case of Mesozoic mammals, there is an extreme sparsity of post-cranial remains, a correlation of this kind cannot presently be made. Another approach involves identifying mammal taxa present in the particular time period during when, and the region where, the footprints were made. However, Clemens *et al.*, (1979, p. 8) caution that "...negative evidence has little value for Mesozoic mammals", and that "the absence of a group of mammals at a particular time and place generally cannot be taken as an indication that it did not in fact

occur then and there."

The Cloverly Formation of Montana and Wyoming has yielded a significant amount of Lower Cretaceous mammalian remains, preserved within concretionary nodules (Clemens *et al.*, 1979, p. 30). Triconodont mammals of the families Amphilestidae and Triconodontidae appear to be the most significant part of this mammalian fauna; however, the amphilestid specimens have a 35 cm body length, excluding the tail (Jenkins *et al.*, 1979), and so are unlikely candidates as trackmakers; neither is the large triconodont, *Gobiconodon* (Jenkins and Schaff, 1988). Some of the smaller triconodonts, known only from jaw fragments, such as *Corviconodon* (Cifelli *et al.*, 1998), might be nearer the appropriate size to produce these footprints. The middle Albian "Paluxian" land mammal age within the Trinity Group of Texas and Oklahoma (Antlers Formation) contains triconodonts (Triconodontidae), multituberculates, symmetrodonts (Spalacotheriidae) and "Theria of metatherian-eutherian grade (Aegialodontidae and Pappotheridae)" (Clemens *et al.*, 1979, pp. 30-31). Triconodonts are also known from teeth and lower jaw remains (approximately 21 mm long) from the Lower Cretaceous Arundel Clay of the Patuxent Formation (Cifelli *et al.*, 1999). The Albian-Cenomanian Cedar Mountain Formation of Utah has likewise produced triconodont mammal remains (Cifelli and Madsen, 1998). Most of these mammals are known solely from their teeth; few post-cranial skeletal remains have been recovered. No Lower Cretaceous mammal remains are known from western Canada (Dr. Donald Brinkman, Royal Tyrrell Museum of Palaeontology, pers. comm., 2000). Consequently, it is not possible to make a better identification of the track-making mammals. It is hoped that continuing work at Grande Cache will lead to the discovery of additional mammal footprints, which may shed more light on the nature of the mammal ichnofauna of the Gates Formation.

Mammalian footprints were earlier reported from the Gething Formation of the Peace River Canyon, and named as *Duquettichnus kooli* by Sarjeant and Thulborn

(1986); however, those were markedly larger and so closely comparable to those of the living Australian brush-tail possum that they are almost certainly marsupial footprints. The newly discovered imprints are quite different in morphology and are the smallest mammalian footprints yet reported from the Mesozoic.

5.0 GATES FORMATION TRACKSITES

From the time of the first report of dinosaur footprints from the Smoky River Coal Mine, to the present at least nineteen tracksites have been recognized from the research area (Figure 5.1).

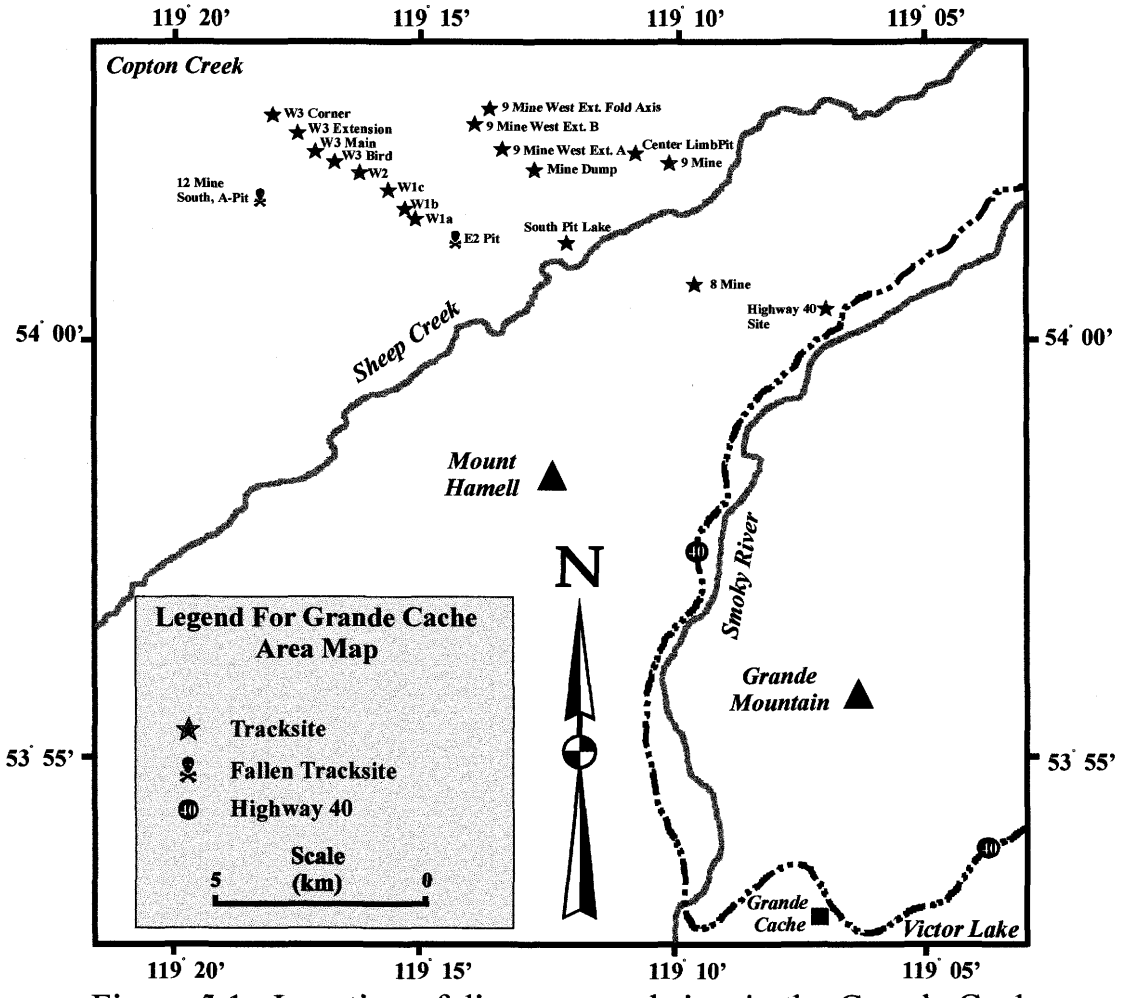


Figure 5.1. Location of dinosaur tracksites in the Grande Cache area, Alberta. Modified from Langenberg *et al.*, (1987).

5.1 W3 Main (N 54° 02.15922' W 119° 16.75121')

Preliminary observations of the W3 Main tracksite were brief (McCrea and Currie,

1998), due mainly to the fact that all observations were taken from the ground in poor weather. The W3 Main site is at an altitude of nearly 1700 meters and is frequently overcast or fogged, which affects the ability of track researchers to discern all the footprints on the footwall. Moreover, the orientation of the footwall is such that the sun only shines on it for part of the day. Even so, it was easy to see that this tracksite was completely different from all other tracksites in the Smoky River Coal Mine. The W3

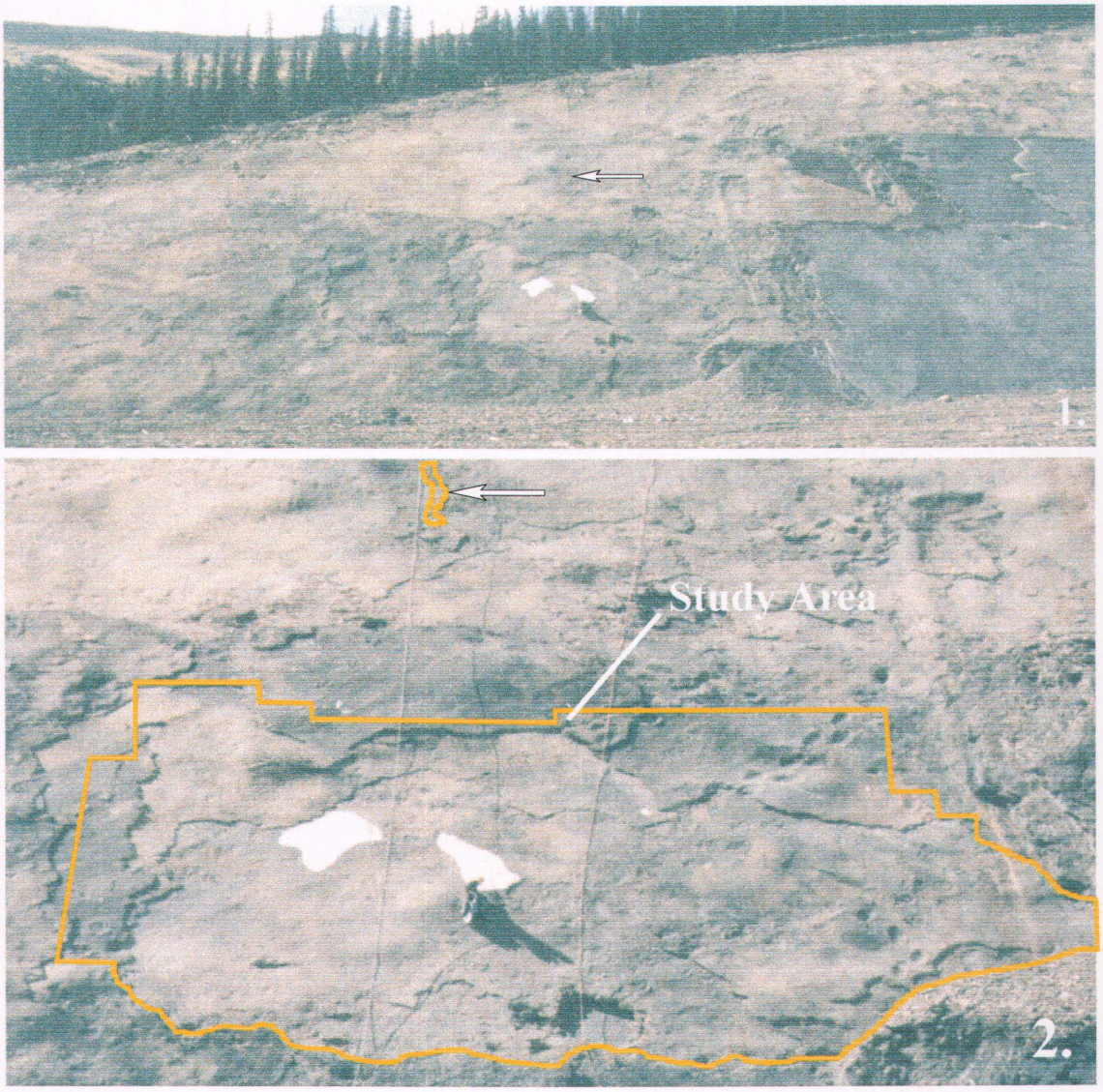


Figure 5.2.1-2: W3 Footwall. 1, W3 MainTracksite; 2, Closeup of study area; white areas are latex peels under preparation (left to right TMP 98.89.1, 2 and 3). Arrows show area from which replica cast TMP 98.89.5 was taken (Figure 4.12). Mark Mitchell (Royal Tyrrell Museum of Palaeontology) is providing scale.

site exhibits the most footprints (estimated at >6000) and has the greatest diversity of ichnotaxa of all the Gates Formation sites in the Smoky River Coal Mine (Figure 5.2.1-2).

The tracksite is situated on a steep (60°) footwall which is >60 m in height (Figure 5.2.1). The main study area was close to the bottom of the footwall and extended upslope >16 m (Figure 5.2.1-2). Footprints and trackways continue to the top of the footwall and extend laterally on both sides a few hundred meters. Footprints are present on several bedding-planes. The sequence of bedding-planes was recorded, and their surface coverage was mapped along with the position of the footprints (Figure 5.3).

Non-biogenic sedimentary features: Prominent ripple-marks are present on the Bedding-planes C and B, but are absent on A. The ripples are anastomosing, with crests 3-7 cm in width and troughs 2-5 cm in width. They are likely to be ripples formed in shallow water by wind action, due to the lack of evidence for water-produced currents such as directional deformation of footprints (where the footprint is smeared in the direction the current was flowing) and because of their similarity to other eolian influenced sediments (Brookfield, 1992). The orientation of the ripple-crests is consistent in Bedding-planes C and B, and is illustrated with bi-directional arrows in Figure 5.3 (Grid G1 and A2). Ripples are found in other layers, above and below the beds considered here, and they are consistently oriented in the same direction. This may be evidence of the prevailing wind direction for this area during the Albian.

Bedding-Planes (Thin Section Study): The bedding-planes that preserve the dinosaur footprints at the W3 Main site were studied in the greatest detail. Samples of the four main track-bearing layers at this site were taken and thin sections were prepared. The mineralogical composition of all beds is similar, indicating that the sediments were derived from the same source; the sediments are mainly composed of sub-angular to sub-rounded quartz grains, chert, highly altered feldspars, organic matter and calcite cement, (Lukasz Skublicki, pers. comm., 2000). There is a medium-bedded (19-21 cm

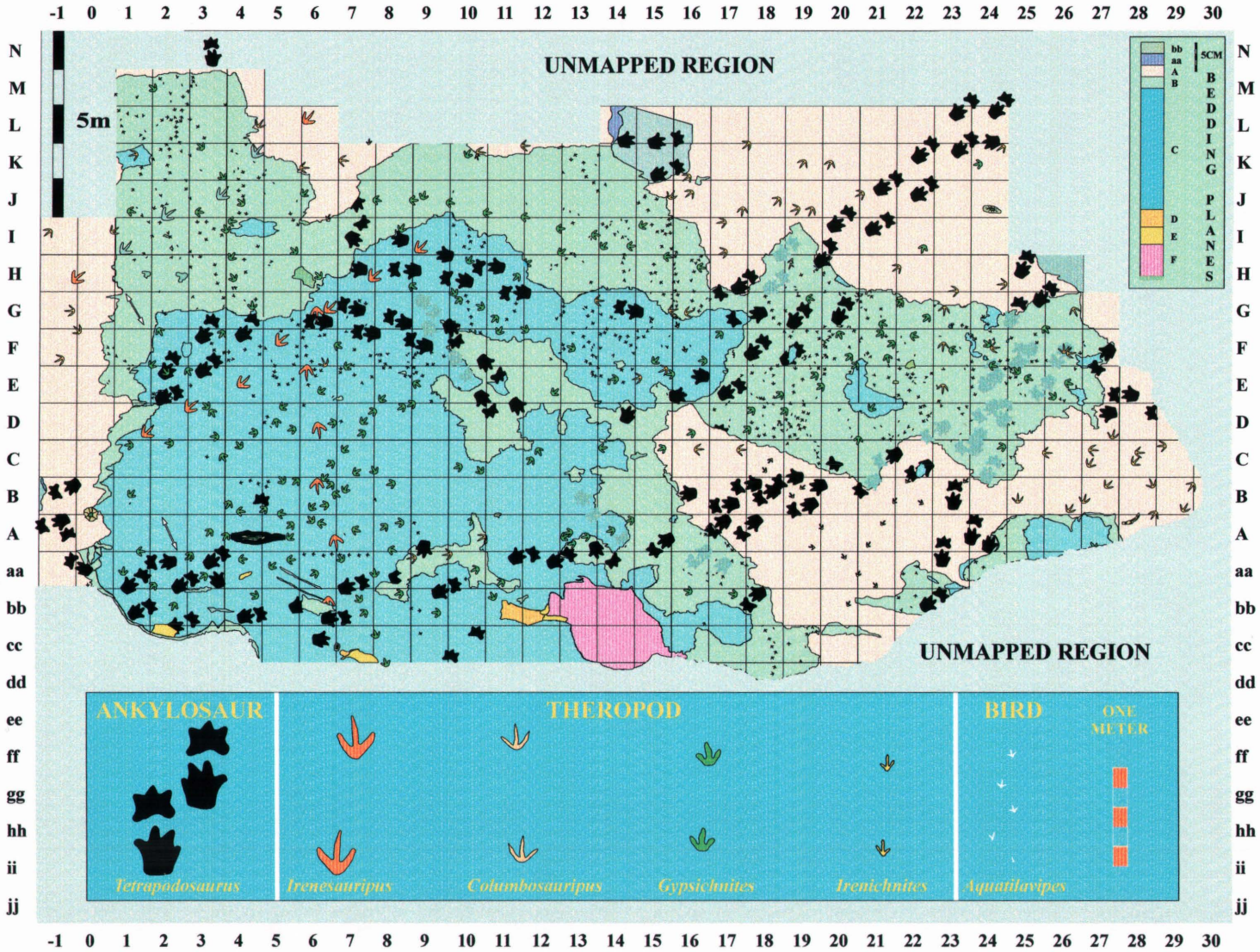


Figure 5.3. Reconstruction of the W3 Main tracksite (study area).

thick) sandstone layer (Bedding-plane C; Figure 5.3) on which a variety of well-preserved dinosaur and avian footprints are also found. This layer consists of laminated, cross-bedded sandstone overlain with a fine silt layer, indicating the settling of sediments during lowstand (Figure 5.4.1). The overlying layer (Bedding-plane B; Fig. 5.4.2) likewise contains well-preserved dinosaur and avian footprints This bedding-plane is 1-2 cm thick and is composed of slightly finer sandstone particles than Bedding-plane C. It is topped with a fine silt layer. Overlying this is another thinly bedded layer (Bedding-plane A; Figure 5.4.3) which is only 1-2 cm thick, and is coarser grained with distinct laminations, displaying graded bedding. Large footprints (*Irenesauripus*, *Tetrapodosaurus* and *Columbosauripus*) are preserved much better than the smaller footprints, indicating that this layer was more resistant to impressions by lighter animals. Bedding-planes aa and bb have vertebrate footprints on them as well, but were a very minor part of this study. However, their mineralogical composition is

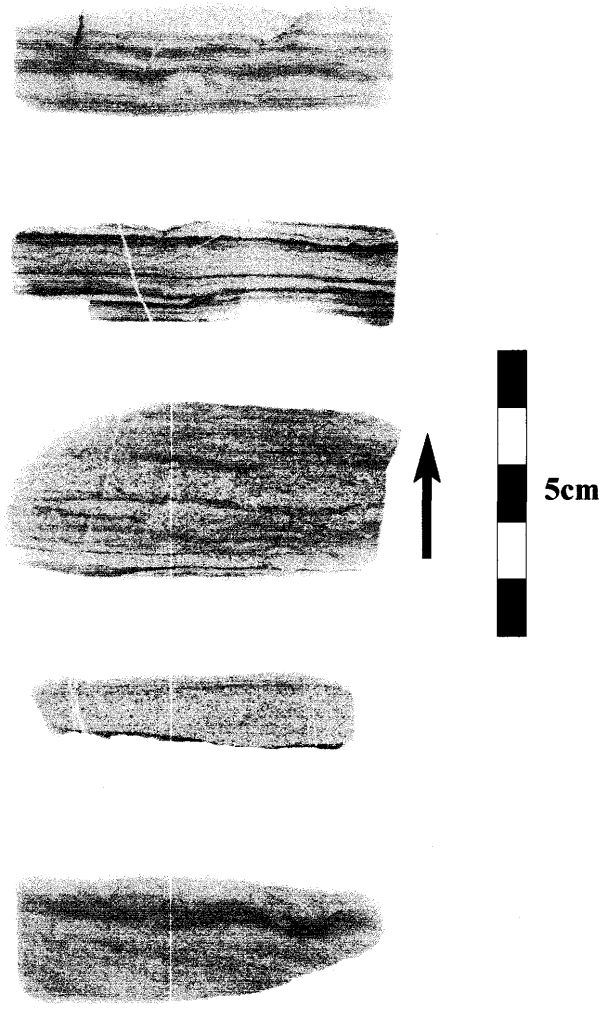


Figure 5.4. Thin sections of vertebrate track-bearing beds at the W3 Main site. Arrow indicates top of beds. 1, Bedding-plane C. 2, Bedding-plane B. 3, Bedding-plane A. 4, Bedding-plane aa. 5, Bedding-plane bb.

similar to Bedding-planes C-A, but they are slightly finer-grained with distinct organic matter layers (Figure 5.4.4-5).

Macro plant remains: There is a substantial amount of carbonized organic debris, most often identifiable as portions of leaves and stems. Often the larger footprints, (those of *Irenesauripus* for example) contain a large amount of plant mulch. These footprints were low areas on the bedding surfaces and trapped floating plant debris.

There are also larger remains of terrestrial plants including *in situ* stumps with radiating root systems, carbonized tree trunks (Figure 5.5.1) and cones. It is likely that the tree trunks (5.5.1) are conifers rather than cycads, since there are many conifer leaves (Figure 5.5.2) in the talus around the W3 footwall, indicating that they were an important component of the flora, or at least had better preservation potential.

The water source that

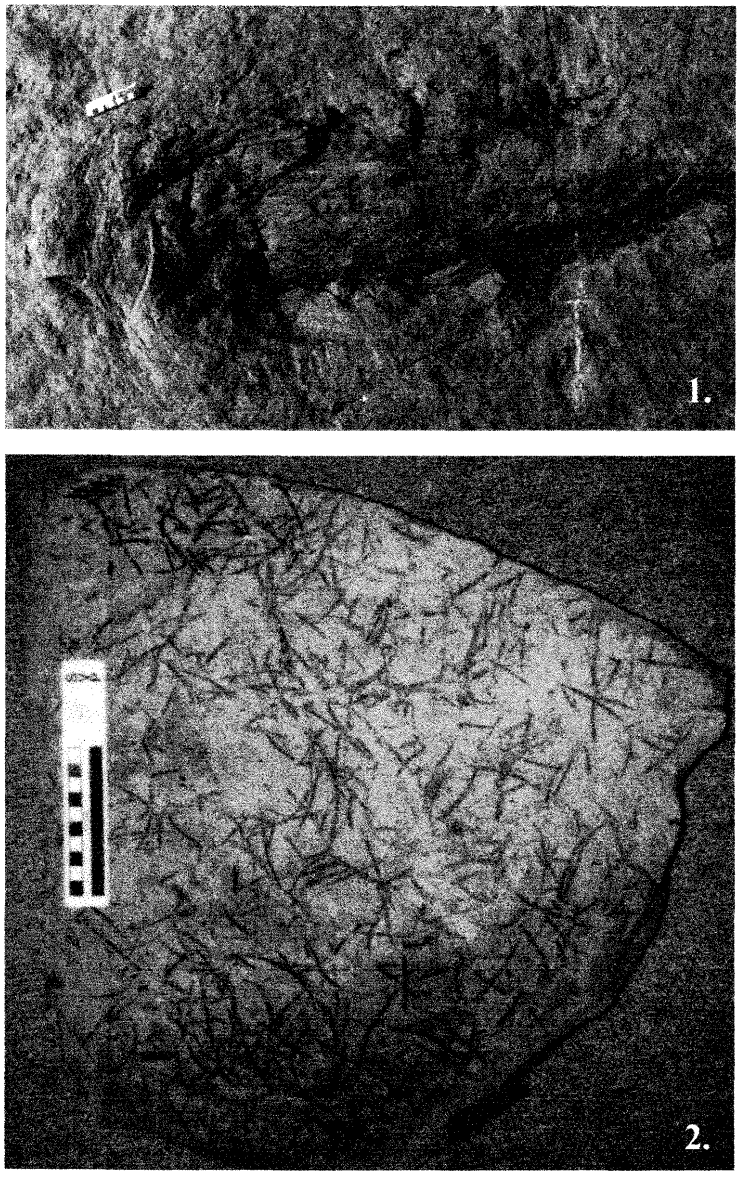


Figure 5.5. Examples of macro-plant fossils on and near the W3 Main Footwall. 1, Fossil stump (possibly conifer) found *in situ* in the grid area of the W3 Main site (Grid A4/5). 2, Fossil conifer needles (*Pityophyllum staratschinii)* found in talus debris near the W3 Footwall.

brought in the sediments could not have been marine, but must have been fresh, because of the *in situ* tree stumps in association with the dinosaur footprints. The tracksite was probably situated close to a river that flooded these low lying areas periodically, though not with high energy influxes, judging by the composition and laminations of the bedding-planes (except Bedding-plane C, which is thick and displays cross-stratification). The conditions seen on the dinosaur trace-bearing beds were eventually succeeded by a coal swamp environment, whose deposits make up the 2-3 m thick No. 4 coal seam (Langenberg *et al.*, 1987).

Vertebrate Ichnofaunal Census: Footprint and trackways can be used to survey the taxonomic diversity and relative abundance of the different trace-makers that are present at a particular site (Lockley, 1986). The length of time available for animals to make footprints is far shorter than the time represented by many sites with skeletal accumulations (Lockley, 1986). Consequently, footprint and trackway based censuses may more closely reflect the composition of the vertebrate community that was present at the time (Lockley, 1986). In a study of modern vertebrate footprints from Africa, Cohen *et al.* (1993) found that most species observed in the study area left a record of footprints, which supports the validity of applying footprint and trackway censuses to ancient tracksites.

The composition of the ichnofauna within the W3 Main study area was recorded for each bedding-plane (Table 12 and 13). Numbers of footprints and trackways (minimum of two prints) were compiled separately in order to graphically illustrate the differences that these two approaches can produce from the same pool of data. The trackway abundance data is probably the most useful, since it involves individual animals rather than the footprints that make up the particular trackway (Lockley, 1986). However, not all footprints could be linked to a specific trackway, so it is also important to include footprint abundance.

The graphic displays of the footprint data compiled from Table 12, show

significant differences in ichnofaunal composition between the three main footprint-bearing bedding-planes (Figure 5.6.1-3). The avian ichnotaxa *Aquatilavipes* ichnosp. 1 dominates the ichnofaunas on Bedding-planes B and C, but only one print was recorded on Bedding plane A. This may be due to the inferred resistance of Bedding-plane C to impressions from lightly-built animals. The presence of a greater number of *Irenichnites* prints (very faint) on this bedding-plane is a bit puzzling in this context. The *Irenichnites* print-maker may have preferred firm substrates. *Tetrapodosaurus* footprints dominate Bedding-plane A, but some of the smaller ichnotaxa may be under-represented, again due to the inferred firmness of the substrate. *Tetrapodosaurus* prints are well-represented on Bedding-planes B and C.

The other ichnotaxa (*Gypsichnites*, *Columbosauripus* and *Irenesauripus*) are represented in varying proportions between the different bedding-planes. *Irenesauripus* prints are found in low numbers on Bedding-planes A and C, and are completely absent (except for underprints) from B. *Columbosauripus*

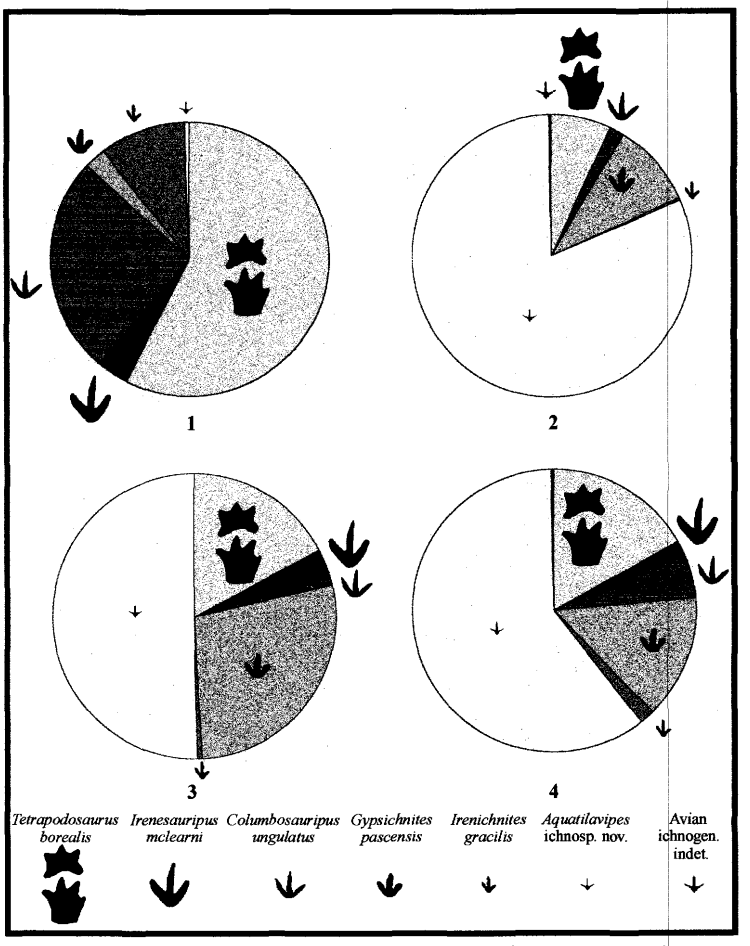


Figure 5.6.1-4: Contribution of each ichnotaxa to the W3 Main ichnofauna based on abundance of foot-prints. Data taken from Table 10 (as percentages). 1, Bedding-plane A. 2, Bedding-plane B. 3, Bedding-plane C. 4, Sum of Bedding-planes A- C.

prints are well represented on Bedding-plane A, but are minor components of B and C. Conversely, *Gypsichnites* prints are well represented on Bedding-planes B and C but are virtually absent from A. So far, no explanation for the variability of proportions of ichnotaxa between the different bedding-planes is apparent.

When all of the footprint data from the three bedding-planes are combined (Figure 5.6.4), the avian ichnotaxa clearly dominate the ichnofauna. *Tetrapodosaurus* and *Gypsichnites* prints are a significant component of the combined ichnofauna, as are *Columbosauripus* prints to a lesser degree. The largest and smallest theropod footprints are very minor components of the ichnofauna.

Trackway percentages vary considerably from footprint percentages but, since they represent individuals, they are commonly used for comparative purposes in census studies and likely correspond to the relative abundance of the footprint-producing animals (Lockley, 1991; Thulborn, 1990). On Bedding-plane A (Figure 5.7.1), trackways of *Columbosauripus* are dominant, while *Tetrapodosaurus* and *Irenichnites* trackways make up a significant percentage of the ichnofauna. *Gypsichnites* and *Irenesauripus* trackways are less common. No bird trackways are present. On Bedding-plane B (Figure 5.7.2), >50% of the trackways were produced by birds. *Gypsichnites* trackways are also very important. *Columbosauripus* and *Tetrapodosaurus* trackways are less abundant. On Bedding-plane C (Figure 5.7.3), *Gypsichnites* trackways make up almost 50% of the ichnofauna; *Tetrapodosaurus* and *Aquatilavipes* ichnosp. nov. trackways divide 40% of the ichnofauna equally between them. *Irenesauripus* trackways are slightly more abundant than those of *Irenichnites*, together comprising a small percentage of the ichnofauna. The combined trackway percentages for all bedding-planes (Figure 5.7.4) show *Gypsichnites* and *Aquatilavipes* ichnosp. nov. trackways as the dominant components of the ichnofauna, with *Columbosauripus* and *Tetrapodosaurus* making up a significant percentage; in contrast, *Irenesauripus* and *Irenichnites* comprise only a small percentage. The combined trackway proportions

(Figure 5.7.4) are compared to other Lower Cretaceous ichnofaunas in North America in Figure 6.2.

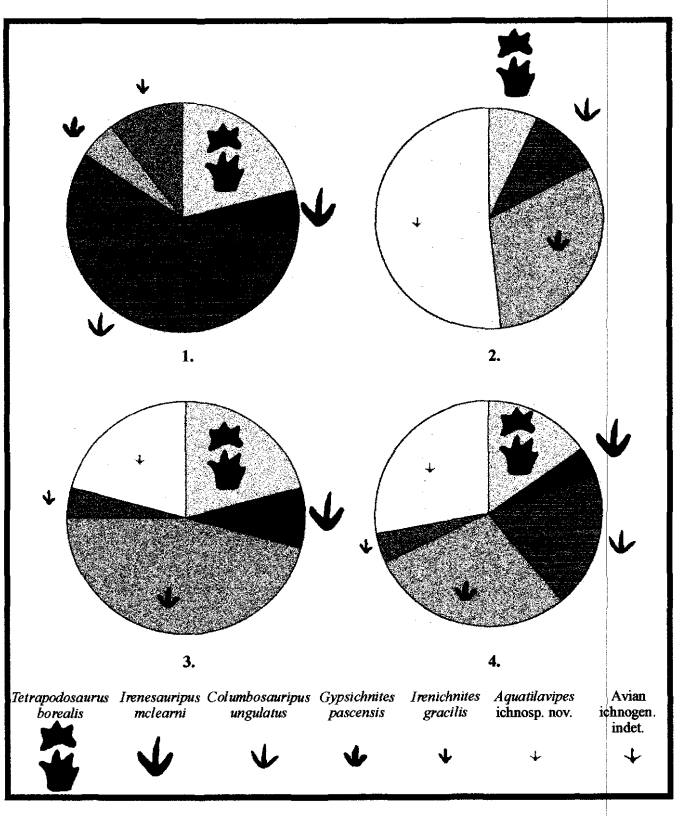


Figure 5.7.1-4: Contribution of each ichnotaxa to the W3 Main ichnofauna based on abundance of trackways. Data taken from Table 11 (as percentages). 1, Bedding-plane A. 2, Bedding-plane B. 3, Bedding-plane C. 4, Sum of Bedding-planes A, B and C.

Predator/Prey Interpretations:

The small percentage of footprints and trackways identified as *Irenesauripus* can be used to support ideas of dinosaur endothermy. Based on studies of predator/prey ratios of modern endothermic and ectothermic animals, Bakker (1986) demonstrated that mammal predator/prey ratios were always low, with large predators comprising about 0.3%. However, fossil predatory mammals from the Eocene made up 4.4% of the mammal population. This study was also applied to the Upper Cretaceous dinosaurs of Alberta where predators were found to be within the mammal range at 3.5% of the population.

Predator/prey calculations were made using footprints from the W3 Main site. With the bird ichnotaxa removed from consideration, only the large predator traces (*Irenesauripus*) and potential prey traces (*Columbosauripus*, *Gypsichnites*, *Tetrapodosaurus* and *Irenichnites*) remain. *Irenesauripus* footprints make up 3.9% of the footprint ichnofauna and 5.8% of the trackway ichnofauna, these figures are close to endothermic community characteristics as set out by Bakker (1986).

Interpretation of Vertebrate Activity: The tracksite map of the W3 Main study area (Figure 5.3) shows the activities of the various footprint-producing animals. The dinosaur ichnotaxa show short to lengthy trackways with little meandering, although there is one abrupt course change in a *Gypsichnites* trackway (Figure 5.3; Grid F2-aa2). The large theropods, represented by *Irenesauripus* footprints, were not abundant. Their trackways show that the animals traveled steadily, but not quickly (Table 1), in a fairly straight line, traversing this depositional environment. Smaller theropods and the presumed ornithopod ichnotaxon *Gypsichnites* were moving at a fast walk to a sprint (Tables 3-5). Some of the smaller dinosaurs would almost certainly have been prey for the theropods responsible for producing the large *Irenesauripus* footprints. The *Tetrapodosaurus* trace-makers proceeded across the substrate at a slow but steady walk (Table 6a and b). The nodosaurs would have been less susceptable to predation due to their armor and defensive shoulder spikes.

The avian ichnotaxa are concentrated in certain areas of the W3 Main site, perhaps gathering around the margins of drying pools in which some of the invertebrate ichnofauna, definitely present in large numbers based upon abundant traces, may have served as food. One *Aquatilavipes* ichnosp. nov. trackway appears to be of a bird taking flight, since the stride and pace lengths increase significantly along the length of the trackway, which then ends abruptly (Table 9a: Trackway G5-F6). There is little direct interaction between the different ichnotaxa in the study area in contrast to other, dramatic tracksite interpretations with predator-prey interactions (Bird, 1944; Thulborn and Wade, 1979).

Trackway orientations: Trackway orientations have been used to demonstrate the existence of gregarious behaviour in extinct animals and also to define shorelines and palaeoslopes (Lockley, 1986; Thulborn, 1990). On level ground, this data can be measured using a compass. On a steep slope, other methods are required. The survey grid was constructed with reference to the strike of the anticline. The baseline of the

grid is perpendicular to the strike, providing a common reference point for trackway orientation calculations and permitting a repeatable procedure. Trackway orientation data for each ichnotaxon and each bedding-plane (Tables 14-17) were taken from measurements of the completed trackway map (Figure 5.3). Rose diagrams were constructed for each ichnotaxon and each bedding-plane (Figures 5.8-5.10).

Bedding-plane A trackways together show a strong bimodal orientation (roughly the top right and bottom left of the rose diagrams). The relatively abundant *Columbosauripus* and *Tetrapodosaurus* trackways demonstrate bimodal orientation for individual ichnotaxa. Bimodal orientation may be an indicator of shoreline in this context (Lockley, 1986).

On Bedding-plane B, *Aquatilavipes* ichnosp. nov. trackways show a strong bimodal orientation. Since they are presumed to be avian, this orientation could be influenced by wind direction.

Bedding-plane C trackway orientations are not as strongly bimodal as those of A, with the exception of the *Tetrapodsaurus* trackways.

Upon grouping all of the trackway orientations of dinosaurs together, it is seen that their trackways were most common in the 0°-90° quadrant and practically absent from the 90°-180° quadrant. There was a strong trackway

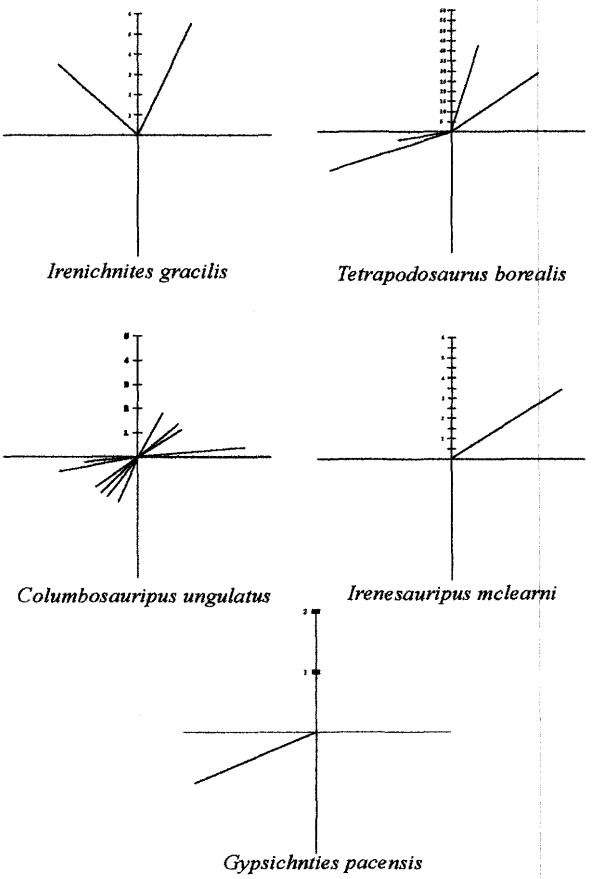


Figure 5.8: Rose diagrams of A-Level trackways, the horizontal axis is parallel to the strike of the slope(100° E, unadjusted).

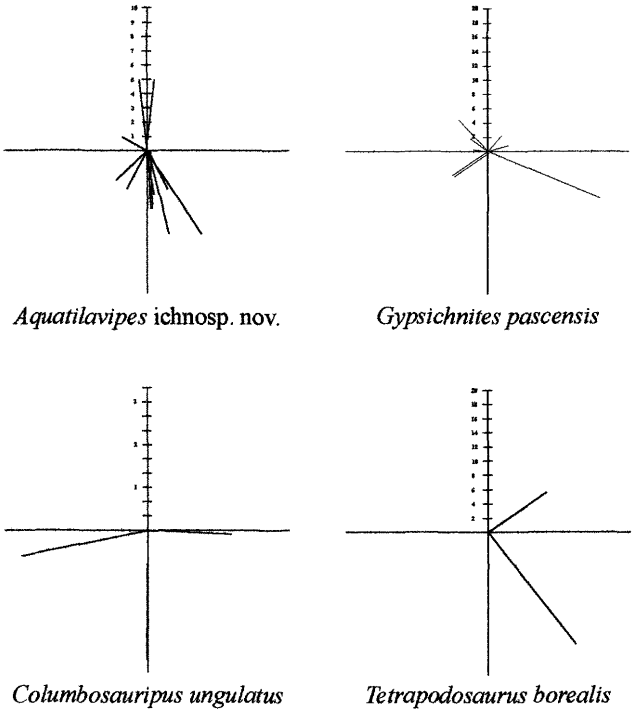


Figure 5.9: Rose diagrams of B-Level trackways, the horizontal axis is parallel to the strike of the slope (100° E, unadjusted).

presence in the 180°-360° quadrants. It is possible that some obstruction, perhaps a shoreline, may have been located in the direction of the 90°-180° quadrant. The bird trackway orientations were not included in this particular comparison, because their movements would not be so greatly affected by the same physical obstructions as the land-bound dinosaurs. However, as noted earlier, their trackways may be useful for interpreting wind direction since their trackway orientations are almost exactly perpendicular to the presumed wind ripple-crest orientations. Birds generally land or take off facing the wind since side winds cause too much turbulent flow and reduce lift. If these birds were large wading birds, as supposed, they would probably have faced the wind to take off, taking a few steps first to build up sufficient speed (Perrins, 1979). If the bird trackway G5-F6 (Bedding plane C) is correctly interpreted as a large bird taking off into the wind, the wind would be coming from approximately 160° on the trackway

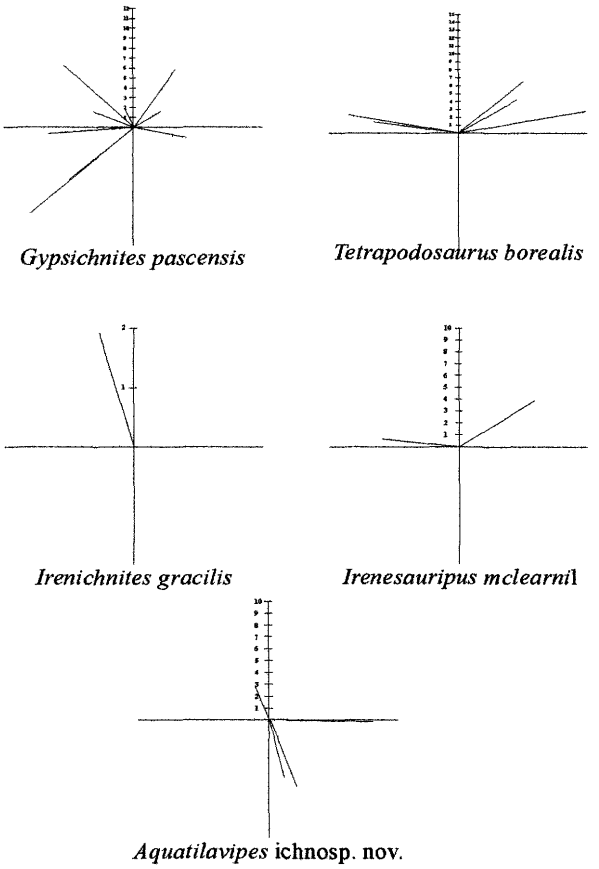


Figure 5.10: Rose diagrams of C-Level trackways, the horizontal axis is parallel to the strike of the slope (100° E, unadjusted).

map (Figure 5.3).

Discussion: Due to the short amount of time available for the study of this large site, not all characteristics of the ichnofauna or the depositional environment could be considered in as much detail as they deserved. However, this study does show that observations of steeply sloping outcrops from the ground can be very misleading, since only the larger ichnotaxa are visible. In this case, between 60% of the footprints would go unnoticed in ideal lighting conditions, and in poor conditions this number would rise to 75% or more.

5.2 Other Gates Formation Tracksites

South Pit Lake (N 54° 01.200' W 119° 12.030')

This was one of the first tracksites to be reported from the property of the Smoky River Coal Mine. The site was reported by mine employees to researchers at the Royal Tyrrell Museum of Palaeontology in 1989 (McCrea and Currie, 1998). The reported specimen was a sandstone block (Figure 5.11) with footprints that appear to have been made by theropod dinosaurs walking across a mud-covered substrate giving them a "five-toed" appearance. Theropod prints generally show only three digits (II to IV), but the soft mud allowed the animal to sink deep enough to preserve digit I (the dew claw)

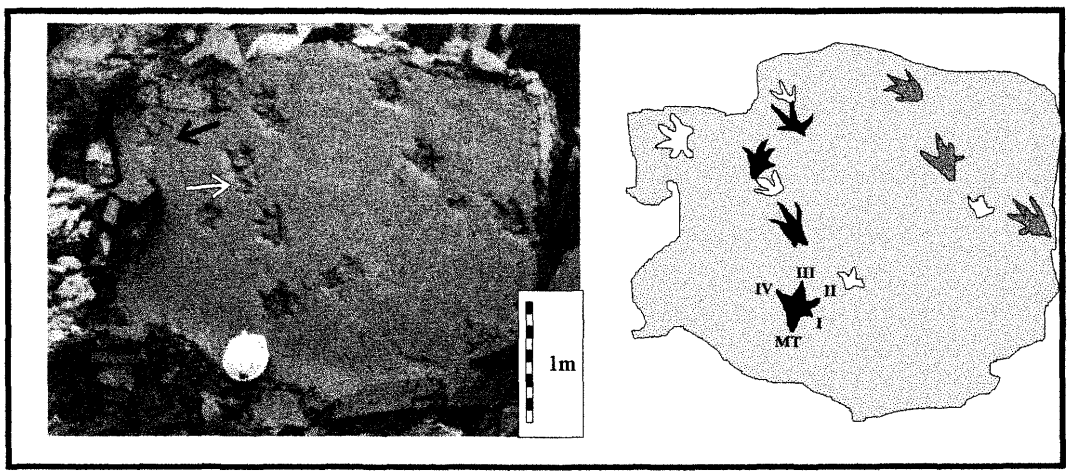


Figure 5.11 Photograph and interpretive drawing of a trackslab with "five-toed" theropod footprints (*Columbosauripus*) from the South-Pit Lake site (TMP 90.27.1). Digits I-IV and the lower portion of the metatarsus (MT) are labelled on the lower-most print (left pes). A *Gypsichnites* print is arrowed (white) and a possible pentadactyl manus (*Tetrapodosaurus*) is also arrowed (black).

and the lower part of the metatarsus (the most posterior "toe"). Gatesy *et al.*, (1999) found similar footprints with the digits I-IV and the metatarsus impressed. Some researchers have also found footprints with digits II-IV and the metatarsus impressed with no trace of digit I (Kuban, 1989; Gierlinski, 1994; 1996).

This block (TMP 90.27.1) also displays a pentadactyl impression (manus) of *Tetrapodosaurus*, an ichnotaxon that is attributable to nodosaurid ankylosaurs (Carpenter, 1984; McCrea and Currie, 1998;. McCrea *et al.*, 1998; McCrea *et al.*, in press, Appendix A). Footprints occur on several bedding-planes at this site. Additional footprint blocks were collected, some with solitary prints (natural cast and natural mould) and some with multiple prints with partial trackways on them (Figures 4.8.1-3). No further research could be conducted at this site since the construction of an explosives complex nearby; which may have covered the footprints.

9 Mine (Lower East Limb Pit): N 54° 02.15920' W 119° 10.04033'

Several *Tetrapodosaurus* trackways along with tridactyl footprint impressions of small bipedal theropods occur on a surface dipping at approximately 40 degrees (McCrea and Currie, 1998; McCrea *et al.*, in press, Appendix A). Staff of the Royal

Tyrrell Museum of Palaeontology excavated one sequence of footprints from this site (McCrea *et al.,* in press Appendix A - Figure 15), a slab of rock containing a manus and pes impression from this trackway being cut out and moved to the museum (TMP 92.107.1). They also recovered some latex peels under difficult conditions (below freezing temperatures) since there was an expectation that this site might be destroyed as a consequence of further mining in the area. However, Smoky River Coal Limited's plans for additional mining in the immediate area were cancelled and this site remains visible today. It has been illustrated in popular literature (Grady, 1993; Psihoyos and Knoebber, 1994)

E-2 Pit: N 54° 01.200' W 119° 14.185'

Footprints from the E-2 Pit footwall were reported to the Royal Tyrrell Museum of Palaeontogy by an employee of Smoky River Coal Limited. The E-2 footwall was considered too unstable for documentation efforts to proceed in safety. Multiple

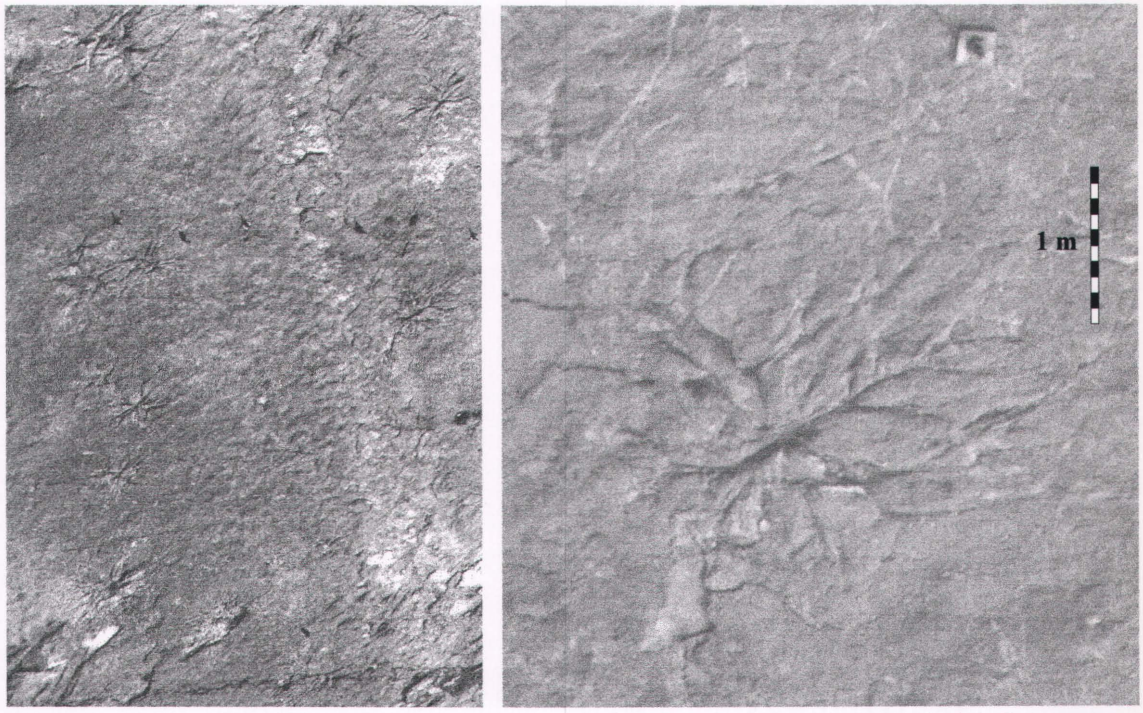


Figure 5.12.1-2: E2-Pit tracksite; 1, *Tetrapodosaurus* trackways meandering between fossil tree stumps and root systems. 2, Close view of a fossil stump with associated roots.

Tetrapodosaurus trackways were found on several consecutive bedding-planes, one of which showed trackways winding around some *in situ* tree stumps (Figure 5.12.1-2). The radiating root systems associated with the stumps are an example of buttress roots, designed for support, and probably indicating a high water table (Scagel, *et al.*, 1984).

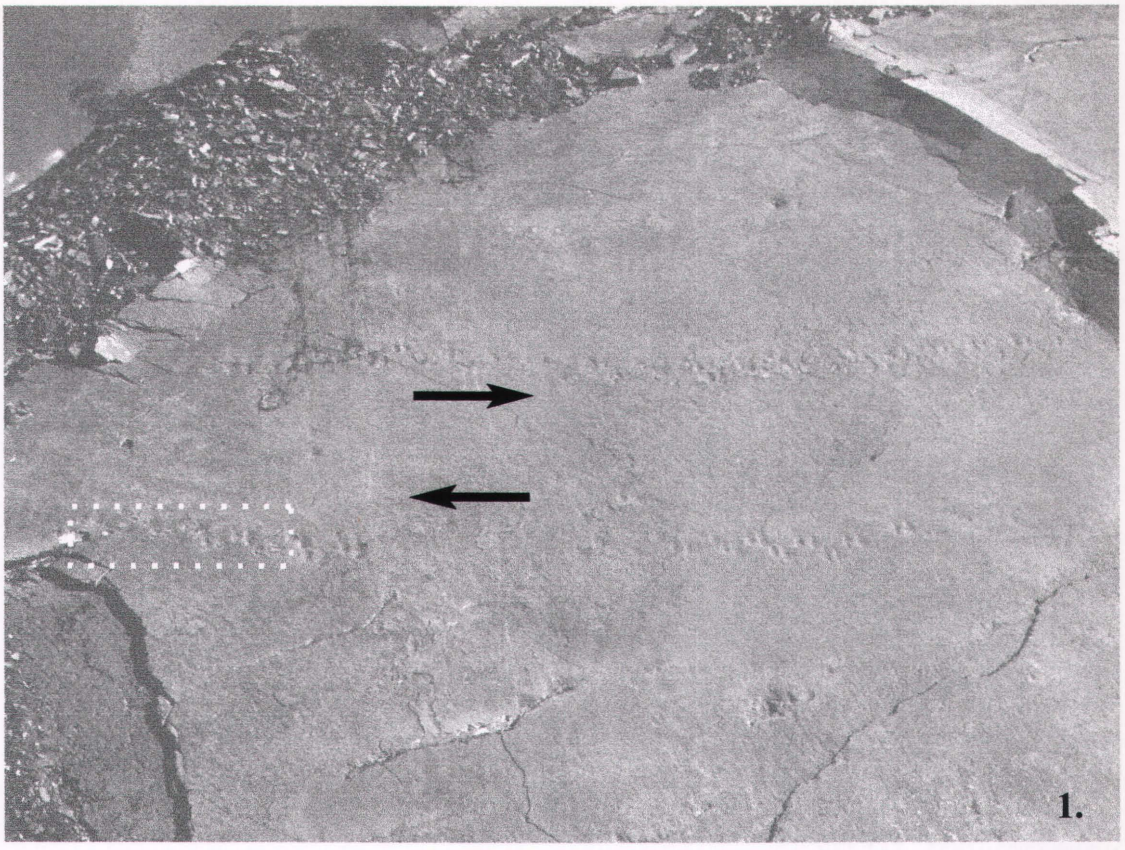
This footprint-bearing section of the footwall failed in a spectacular way on July 4, 1991 during a photo shoot for National Geographic (Psihoyos and Knoebber, 1994, p. 189). A thousand or more footprints were lost in this incident, made inevitable by the removal of the overburden and the steepness of the slope.

12 Mine South, A-Pit: N 54° 01.732' W 119° 18.097'

An estimated 500 footprints belonging to the ichnogenus *Tetrapodosaurus* were exposed after a localized slope failure occurred on a footwall. Initially, observations could only be made at a distance, but even so it could be seen that there were a significant number of footprints on the footwall. The A-Pit footwall is at a 40 degree angle and is the south-facing limb of the same anticline as the W3 corner - E2 Pit limb (Figure 5.1). The footprints were found on a 144 m x 45 m section of the footwall at a height of 30 meters above the floor of the pit. There were at least eight trackways of *Tetrapodosaurus*, the longest trackway containing nearly 120 consecutive manus and pes prints (Figure 5.13.1-2) thus making it the longest known ankylosaur trackway (McCrea and Currie, 1998; McCrea *et al.*, in press, Appendix A).

The lithology is a richly organic, fine to medium-grained, ripple-marked sandstone with evidence of what must have been a very active infauna, indicating that these sediments were formed in a shallow, low-energy environment. Previous studies of the bivalve layers and microfossil assemblages above the Number 4 coal seam suggest that some of these sediments were formed in a brackish, coastal-plain or deltaic depositional environment (Langenberg *et al.*, 1987). Some remains of *in situ* tree stumps were also present.

Many of the footprints were infilled with limonite-rich sediment; this imparted an



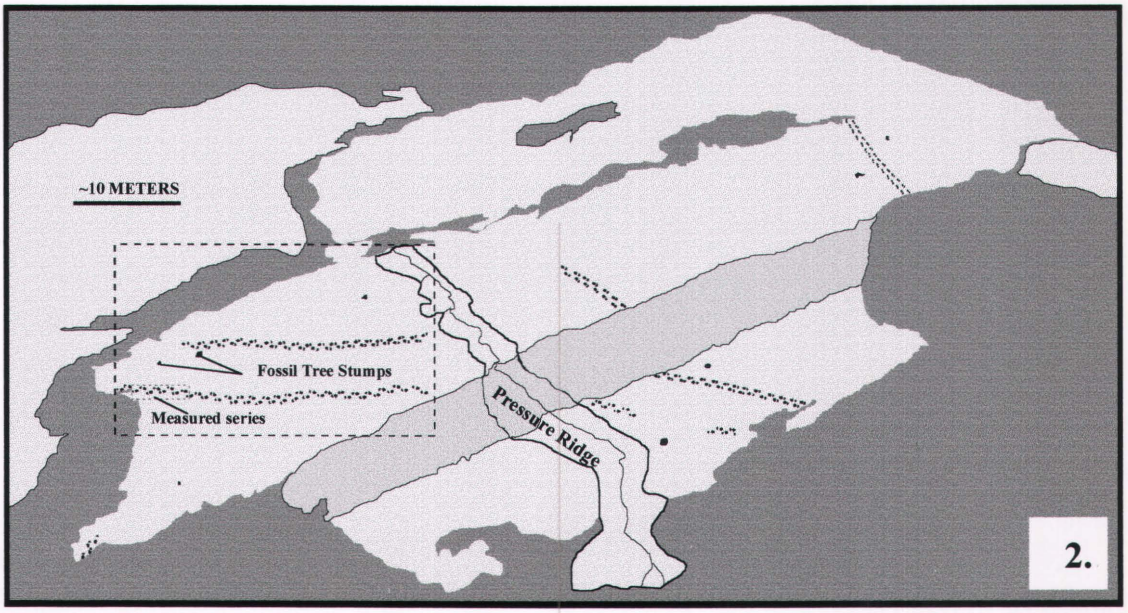


Figure 5.13.1-2: 1, Photograph of a portion of the 12 Mine South, A-Pit tracksite. 2, Illustration of the 12 Mine South, A-Pit, *Tetrapodosaurus* tracksite. Note: The formation of the pressure ridge figured split the two longest trackways almost in half. The dotted line indicates section of trackway that some measurements were taken. The dashed line encloses the photographed area illustrated in 5.13.1.

Figure 5.14. W1b tracksite. Two parallel *Tetrapodosaurus* trackways (other trackways not figured). Sandra Jasinoski is providing scale.

over 33%. The dinoturbated site extends for about 200 meters along the length of the mining road. It is hard to imagine all of these traces being produced by only a few animals. Dinoturbated sites strongly indicate some type of gregarious behavior in the footprint-producing species (Lockley, 1991).

W1b: N 54° 01.816' W 119° 15.315'

Very close to the W1a site, and stratigraphically about 20 cm above it, is a limited exposure of a friable fine-sand substrate. There are at least three trackways of *Tetrapodosaurus* prints, displaying distinct footprints with good preservation of manual and pedal digit impressions (McCrea *et al.,* in press, Appendix A). Two trackways on the same bedding-plane are proceeding in parallel orientation (Figure 5.14), suggesting gregarious behavior.

W1c: N 54° 02.020' W 119° 15.697'

A relatively small exposure with several *Tetrapodosaurus* footprints in at least two trackways (McCrea *et al.*, in press, Appendix A).

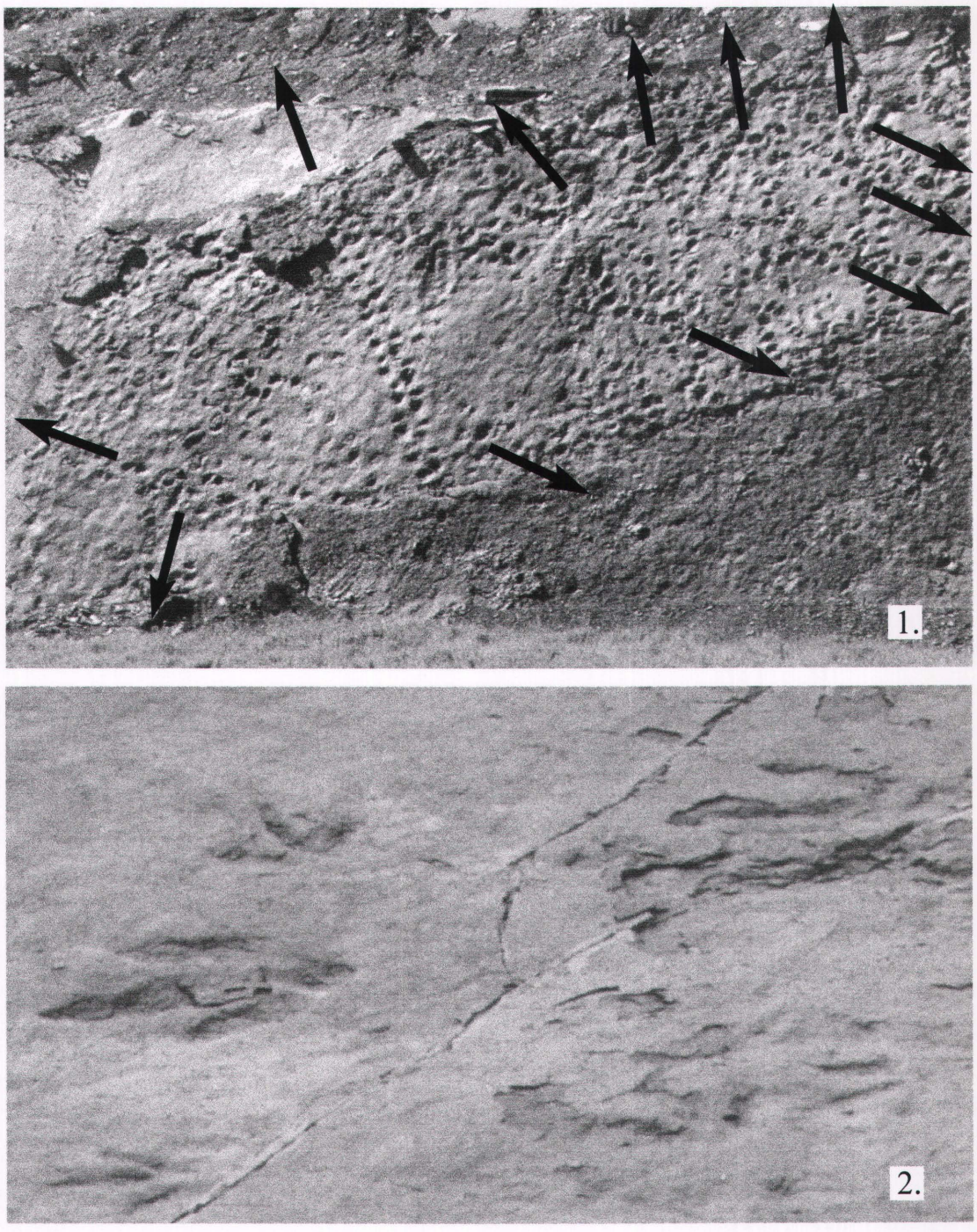


Figure 5.15.1-2: W2 tracksite; 1, Multiple *Tetrapodosaurus* trackways (arrows indicate direction of travel. 2, Theropod footprints (*Irenesauripus* and *Columbosauripus*) from the W2 site. For the purpose of scale, the *Irenesauripus* footprints are close to 50 cm in length.

W2: N 54° 02.089' W 119° 16.110'

A large tracksite with a moderately dinoturbated substrate (Figure 5.5.1). The ichnofauna is overwhelmingly dominated by *Tetrapodosaurus* footprints, but there are also *Irenesauripus*, *Gypsichnites* and *Columbosauripus* footprints in small numbers (Figure 5.5.2). Footprints occur on multiple bedding-planes, some of which are moderately dinoturbated, but others show only a few vertebrate traces. Some *Tetrapodosaurus* trackways are oriented parallel to each another (Figure 5.5.1), suggesting gregarious behavior (McCrea *et al.* in press, Appendix A). There are two sets of three trackways with consistent distances between individual trackways, which may indicate how these animals spaced themselves when travelling in a group.

W3 Bird: N 54° 02.136' W 119° 16.664'

Located on the shoulder of the W3 footwall, and lying stratigraphically above the W3 Main site, there is a sandstone bedding-plane with an orange weathering surface (limonite) where exposed (Figure 5.16 - black arrow). Through minor failures of this bedding plane, some blocks have broken splitting the bedding-plane revealing numerous small tridactyl prints as natural cast and moulds (Figure 4.11.1-2). The prints range in size from 9 cm to 4 cm and are referable to the ichnogenus *Aquatilavipes*, representing a

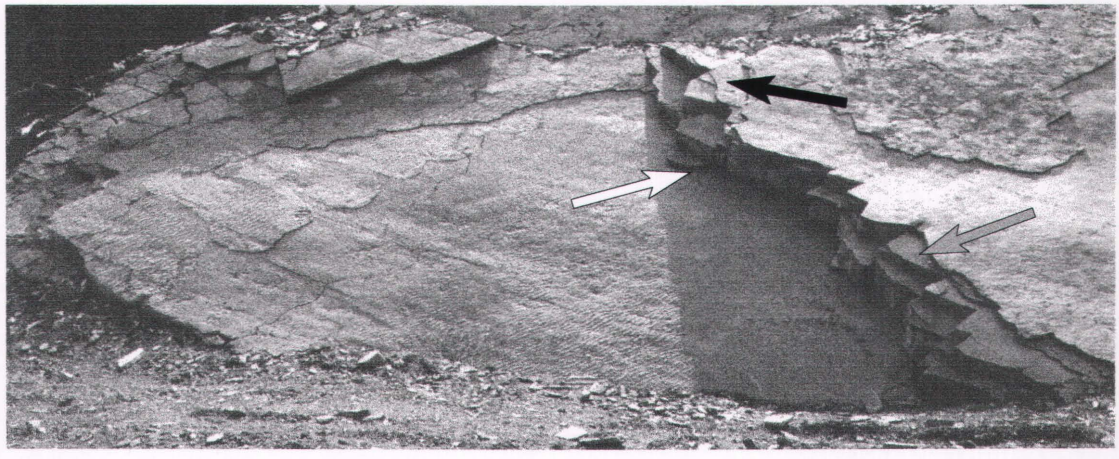


Figure 5.16. W3 bird site. The black arrow indicates the particular bedding-plane from which many bird footprints (natural casts and natural moulds). The white arrow shows the direction of the large bipedal trackway (?*Irenesauripus*). The gray arrow indicates the location of a solitary *Gypsichnites footprint*.

new ichnospecies from that described earlier. The bird footprint-bearing bed is extensively exposed. There is also one *Gypsichnites* footprint on a bed that has been correlated with Bedding-plane C of the W3 Main site (Figure 5.16 - grey arrow). In addition, there is a trackway of a large biped (?*Irenesauripus*) distorted by ripple marks on a large surface exposure (Figure 5.16 - white arrow).

W3 Extension: N 54° 02.290' W 119° 17.057'

This site is close to the W3 Main site and is at the same stratigraphic level. There are *Tetrapodosaurus* trackways in relative abundance, as well as *Irenesauripus* and *Columbosauripus* prints. A natural cast (TMP 99.49.2) of a *Tetrapodosaurus* manus (left) was collected from this site (McCrea *et al.,* in press, Appendix A). There are some small avian-like footprints preserved as natural molds near one *Tetrapodosaurus* trackway; these are 3.5 cm in length, with very narrow, stick-like digits and wide divarication. Some of the footprints are deeply incised into the substrate, while others are quite faintly impressed.

Figure 5.17. 9 Mine West Extension Fold Axis site. Arrow indicates where *in situ* natural moulds of *Tetrapodosaurus* prints were found.

W3 Corner: N 54° 02.312' W 119° 17.161'

A recently discovered site similar to the W3 Main and the W3 Extension site. There are several *Tetrapodosaurus* trackways (McCrea *et al.,* in press, Appendix A), as well as several trackways of tridactyl bipeds (*Irenesauripus* and *Columbosauripus*).

9 Mine West Extension, Fold Axis: N 54° 02.433' W 119° 13.552'

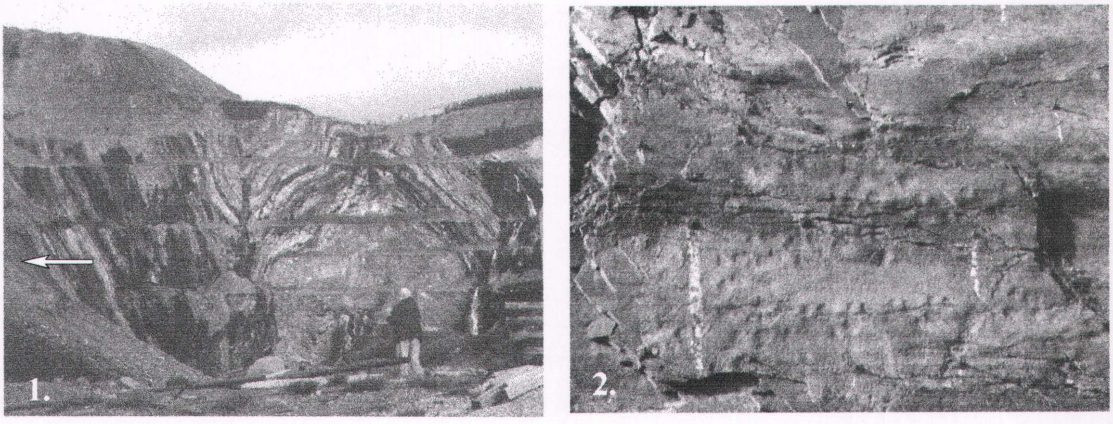


Figure 5.18. Center Limb Pit Site; 1, View of excavated anticline; arrow indicates location of footprint site (Dr. W.A.S. Sarjeant is providing scale). 2, View of footprint surface with footprints of *Tetrapodosaurus borealis*.

A few *Tetrapodosaurus* footprints were found at this tracksite, the only site to date that has been found on level ground (McCrea *et al.*, in press, Appendix A). The trace-bearing surface is lightly covered with mud and other debris, which has filled in most low-lying areas, including footprints (Figure 5.17). Several other tracksites are located on the south-west limb of this anticline (Figure 5.1).

Center Limb Pit: N 54° 01.930' W 119° 10.700'

A site discovered in the summer of 1999 (Figure 5.18.1-2) which displays several *Tetrapodosaurus* trackways on one limb of an anticline (McCrea *et al.,* in press, Appendix A). The anticline fold axis was mined for coal, which accumulates in great thicknesses in these structures.

Mine Dump (9 Mine): N 54° 01.88272' W 119° 12.38350'

Figure 5.19.1-2: Mine Dump site; 1, Erosion along the anticline limb (Dr. Roland Gangloff and Mr. Kevin May providing scale). 2, Natural casts of *Tetrapodosaurus* prints; manus (top left) and pes (upper right center and bottom left). Pes in upper right was collected (TMP 97.5.20).

Several natural casts of *Tetrapodosaurus* footprints (manus and pes) are eroding from the top of a high slope (Figure 5.19.1-2). One pes print (TMP 97.5.20) was collected from this site (McCrea and Currie, 1998; McCrea *et al.,* in press, Appendix A).

9 Mine Extension a: N 54° 02.189' W 119° 13.538'

There are two *Tetrapodosaurus* trackways situated high on the anticline limb. These trackways have only been observed from a distance (McCrea *et al.*, in press, Appendix A).

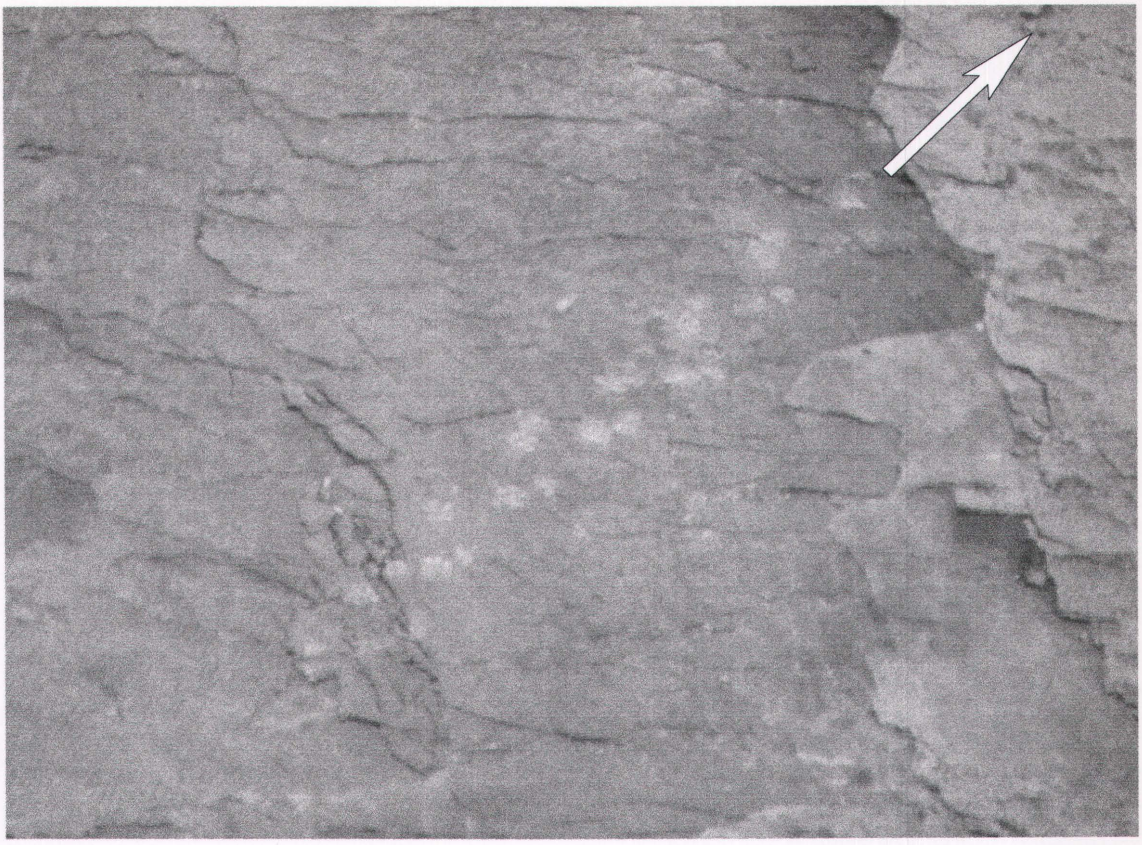


Figure 5.20. 9 Mine West Extension b tracksite; Solitary *Tetrapodosaurus* trackway. Footprints are orange (stained with limonite) against the gray, rippled substrate. White arrow indicates direction of travel.

Figure 5.21. Two *Aquatilavipes swiboldae* footprints from the Highway 40 tracksite of the Gladstone Formation (Gething equivalent).

orange color to the prints, making them stand out against the gray sandstone. Some of the infillings were removed during the course of this study revealing pyrite crystals which had formed between the mold and the infilling. The gray sandstone substrate in which the footprints were preserved was highly organic and was evidently in an area of poor drainage, leading to anaerobic decay and sulphate reduction, allowing the formation of the pyrite crystals (Collinson, 1996).

The two longest trackways at this site lie parallel but proceed in opposite directions (Figure 5.13.1-2). The inverse orientation of these trackways could be evidence of progression along a shoreline (Lockley, 1986). However, the presence of a very shallow *Tetrapodosaurus* trackway, cutting perpendicularly across the two long trackways may indicate that the inverse orientation may have been influence by some palaeoenvironmental control other than a shoreline; perhaps this was merely a preferred route. It is worth noting that a portion of the long trackways (not figured) appears to be smeared perpendicular to the direction of progression, suggesting the presence of an ancient water channel. The track-bearing portion of the A-Pit footwall failed during the summer of 1998, and has since be buried by backfill operations.

8 Mine: N 54° 00.69021' W 119° 09.40625'

A few faint footprint impressions were discovered in October, 1996, on ripple-marked sandstone on the face of a steep water-filled pit in October, 1996 (McCrea and Currie, 1998). At the time, newly fallen snow did not permit examination of the prints. A subsequent visit in the summer of 1997 enabled closer examination of the prints, which were identified as *Tetrapodosaurus* (McCrea *et al.*, in press, Appendix A).

W1a: N 54° 01.719' W 119° 15.274'

This site has a dense covering of footprints belonging to the ichnogenus *Tetrapodosaurus* (McCrea *et al.*, in press, Appendix A). In most places, it is difficult to distinguish the prints and trackways of solitary animals in most places. Using a dinoturbation index developed by Lockley (1991 - fig11.4), the degree of trampling is

9 Mine Extension b:

There is a solitary *Tetrapodosaurus* trackway; which has only been observed from a distance (McCrea *et al.*, in press, Appendix A). Some of the footprints appear to be infilled with a light orange mineral, possibly limonite, comparable to those observed in footprints from the 12 Mine South, A-Pit site (McCrea and Currie, 1998). It is unlikely that these prints will ever be fully documented.

Highway 40: N 54° 00.350 W 119° 06.790

As discussed previously, this site had *in situ* natural casts of *Aquatilavipes swiboldae* prints; these were collected and are stored at the Royal Tyrrell Museum of Palaeontology (Figure 5.21). They were the first confirmed record of bird footprints from Alberta, but were from the Gladstone Formation (Gething equivalent), not the Gates or Cadomin Formations as had previously been reported (Lockley, *et al.*, 1992; McCrea and Currie, 1998).

6.0 DISCUSSION AND CONCLUSIONS

6.1 Distribution of Ichnotaxa in the Gates Formation Tracksites

There are eighteen vertebrate tracksites in the Smoky River Coal Mine; together, they show a large diversity of dinosaurs, birds and mammals. However, the ichnotaxa are unevenly distributed. The Smoky River ichnofauna of the Gates Formation is dominated by *Tetrapodosaurus* footprints, which are found at all tracksites. Eleven tracksites only have *Tetrapodosaurus* footprints.

All of the other vertebrate ichnotaxa (with the exception of the South Pit Lake and the 9 Mine site) are found in five sites that occur in a line on the W3 Corner/E2-Pit anticline limb. These are: W3 Corner, W3 Extension, W3 Main, W3 Bird and the W2 site (Figure 5.1). Though *Tetrapodosaurus* footprints again dominate these five sites to varying degrees (with the exception of the W3 Main site), a pattern is discernible. The W3 Corner-E2 Pit anticline limb is nearly four kilometers in length, from northeast to southwest. The tracksites along this anticline limb have not been correlated, but all were exposed by the removal of the Number Four Coal Seam and (based on observations at the W3 Main site) occur two to three meters below it. The W3 Corner and W3 Extension sites have *Tetrapodosaurus* footprints, as well as large to medium theropod footprints and small bird footprints. At the W3 Main site, tridactyl dinosaur and avian footprints are dominant. At the W2 site, *Tetrapodosaurus* footprints are overwhelmingly dominant, but there are a few *Irenesauripus*, *Columbosauripus* and *Gypsichnites* trackways present (Figure 5.15.1-2). From the W2 site to the E2 Pit (2.7 km), no tridactyl ichnotaxa can be seen, even though there are four tracksite exposures of comparable extent to the W2 and W3 sites. These sites have not been as closely

studied as the W3 Main site, but close observations have been made of at least parts of these tracksites and no tridactyl ichnotaxa have been found. There are two ways to explain this apparent disparity:

1. Vertebrates capable of producing the tridactyl footprints were not living in the area.

From the diversity of ichnotaxa present at the W3 Corner to W2 sites, we know that a diverse vertebrate fauna was definitely present and was within a few kilometers of all tracksites along the anticline limb.

2. Vertebrates capable of producing tridactyl footprints did not enter this area.

Tridactyl vertebrates were either unwilling or unable to go into these areas. Cohen *et al.*, (1993) in their census study of modern vertebrate footprints from Tanzania, observed that footprint proportions differed from observed proportions of the animal populations known to reside in the study area. They explained that there would be a bias "towards greater numbers of depositional environment generalists and away from habitat-specific animals" (Cohen *et al.*, 1993). Perhaps the animals that produced *Tetrapodosaurus* prints - nodosaurid ankylosaurs - are an example of depositional environment generalists.

From preliminary observations, a lateral shift in facies occurs between the W3 Extension-W2 tracksites and the W1c-E2 Pit tracksites. The W3 Extension-W2 tracksites are of similar lithology, primarily laminated fine sands with a moderate amount of organic material. There is evidence of some water currents (cross-bedding in Bedding-plane C) and multiple influxes of sediment (higher energy) in the W3 Extension-W2 section of the anticline. The lithology of the W1c-E2 Pit section is somewhat different, being more fine-grained in texture (low energy) and much darker due to organic content (more coaly). The *Tetrapodosaurus* footprints at these sites show that the substrate contained more water since there are mud bulges. At the E2 Pit, the *Tetrapodosaurus* trackways wend their way between trees, whose trunks are preserved and whose roots radiate laterally. This lateral placement of the roots is a good indication

of the position of the water table: it was very near the surface. It appears that the environment changes from that of a mildly high energy environment with lower plant productivity (W3 Corner-W2) to a low energy environment with higher plant productivity (W1c-E2 Pit). The W3 Corner-W2 sites may have been closer to a river that flooded the area periodically. The W1c-E2 Pit area was a lower energy, backwater area with an abundant plants (i.e. a swamp).

Why would the *Tetrapodosaurus* trace-makers be going into these areas? Ankylosaurs are large herbivores that would constantly seek food (Tiffney, 1997; Chin, 1997). The large numbers of *Tetrapodosaurus* trackways present in the Smoky River Coal Mine could be the result of this quest. Ankylosaurs had rather primitive teeth compared to other herbivorous dinosaurs (Figure 6.1.1), lacking the powerful chewing batteries of the ceratopsians and hadrosaurs (Figure 6.1.2-3). Ankylosaur teeth would have been incapable of handling tough, woody plants or plants with high silica content; they would have preferred softer, non-abrasive plants (Ryan and Vickaryous, 1997; Fastovsky and Weishampel, 1996). Angiosperms were present, but are only represented by three fossil species, none of which are abundant (Wan, 1996). Gymnosperms (conifers and cycads) occur in the Gates Formation (Wan, 1996) but would make tough food (Tiffney, 1997). Anylosaurs had a low browsing range, not much more than a metre or two above the ground (Carpenter, 1997b; Ryan and Vickaryous, 1997; Fastovsky and Weishampel, 1996). The nodosaurid rhamphotheca (beaks) were narrow, perhaps enabling them to be very selective feeders (Carpenter, 1997a). Their large, broad bodies indicate that a significant portion of their internal space was devoted to digestion via bacterial fermentation; some had stomach stones to aid in mechanical digestion (Bakker, 1986; Carpenter, 1997b). Currie (1997), however cautions that the presence of stomach stones is consistently reported in only a few dinosaur groups. Ankylosaurs probably would have preferred a diet of soft herbaceous plants - plants such as ferns, which grow in shady, well-watered or even boggy areas due to their amphibious

life cycle (Tiffney, 1997). Ferns were certainly present in the Gates Formation (Wan, 1996).

The ankylosaurs represented in the Gates Formation were well-adapted to forage in soggy environments. From studies of *Tetrapodosaurus* footprints at the Smoky River Coal Mine, it seems that the morphology of ankylosaur feet is improperly understood. Some museum interpretations give their feet a very elephantine look. This type of foot morphology is designed to function in a specific environment. Elephants - *Loxodonta africana,* for example - are primarily terrestrial animals that have heavily padded feet (Figure 6.2.1-2) to support the weight of their heavy bodies (5,000 - 7,500 kg) on dry land (Walker *et al.*, 1975). Ankylosaur digits (manus and pes) are not

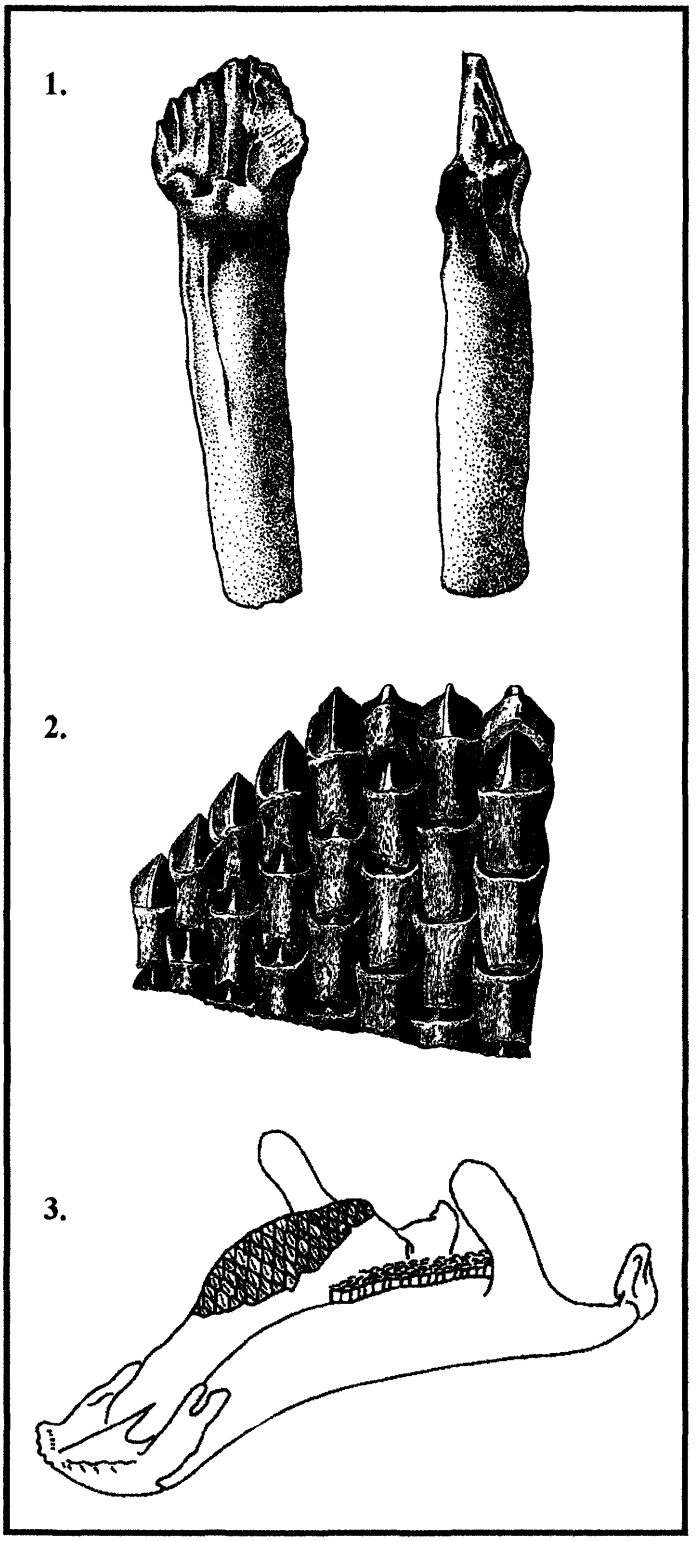


Figure 6.1.1-3: 1, Two views of a nodosaurid tooth; From Coombs and Maryańska (1990). 2, Ceratopsian tooth battery; From Dodson (1996). 3, Hadrosaur tooth battery in lower jaw; From Norman (1985).

spread (Table 6c), maximizing surface area somewhat in the fashion snowshoes or skis. This type of foot is ideal for supporting great weight on soggy, unconsolidated substrates and may have allowed the ankylosaurs to forage for their food without getting mired down. The ankylosaur foot morphology has a modern parallel in the hippopotamus - *Hippopotamus amphibus* - (Figure 6.2.3). The hippopotamus is large (3,000 - 4,500 kg) and primarily aquatic (river habitat), but does come on land to forage for its food (Walker *et al.*, 1975). Its digits are much freer of enclosing flesh than those of elephants. They can also maximize the spread of their digits to give them support in watery environments (Bakker, 1986). This is not to imply that ankylosaurs were as aquatic as the hippos, but it does mean that they were able to exploit environments that other large vertebrates would not be able to enter.

To demonstrate why the tridactyl dinosaurs may not have ventured into overly soggy substrates, a comparison of weight/surface area estimates has been calculated (Table 15). There are several ways to estimate the mass of dinosaurs. One method uses the circumference of the femur, and also the humerus in the case of quadrupeds (Anderson *et al.*, 1985); another estimates the volume of a dinosaurs using a scale models submerged in a water-filled container on a balance (Colbert, 1962; Alexander, 1999). In the latter instance, the estimate of volume depends on the accuracy of the scale model, which in turn depends on the model maker's judgment of how much flesh was carried on the bones of the animal in question (Alexander, 1997). This, in turn, is dependent on prevailing ideas about dinosaur physiology.

The weight/surface area estimates were calculated using mass estimates of the presumed trace-makers taken from Damuth (1994). Damuth (pers. comm., 2000) states that his mass estimates were calculated based on femur and humerus circumference. For the purpose of this exercise, the *Columbosauripus* footprint-maker is identified as a medium theropod and assigned a mass of 750 kg. Footprint surface area measurements were taken from the dinosaur ichnotaxa present in the Smoky River Coal mine (Table

enclosed in a fleshy pad and are quite free of enclosing flesh until they unite proximally with the rest of the foot. It is likely that the caudal portion of the pes did have a substantial fleshy pad (Carpenter, 1984). The digits of the manus and pes are often well-

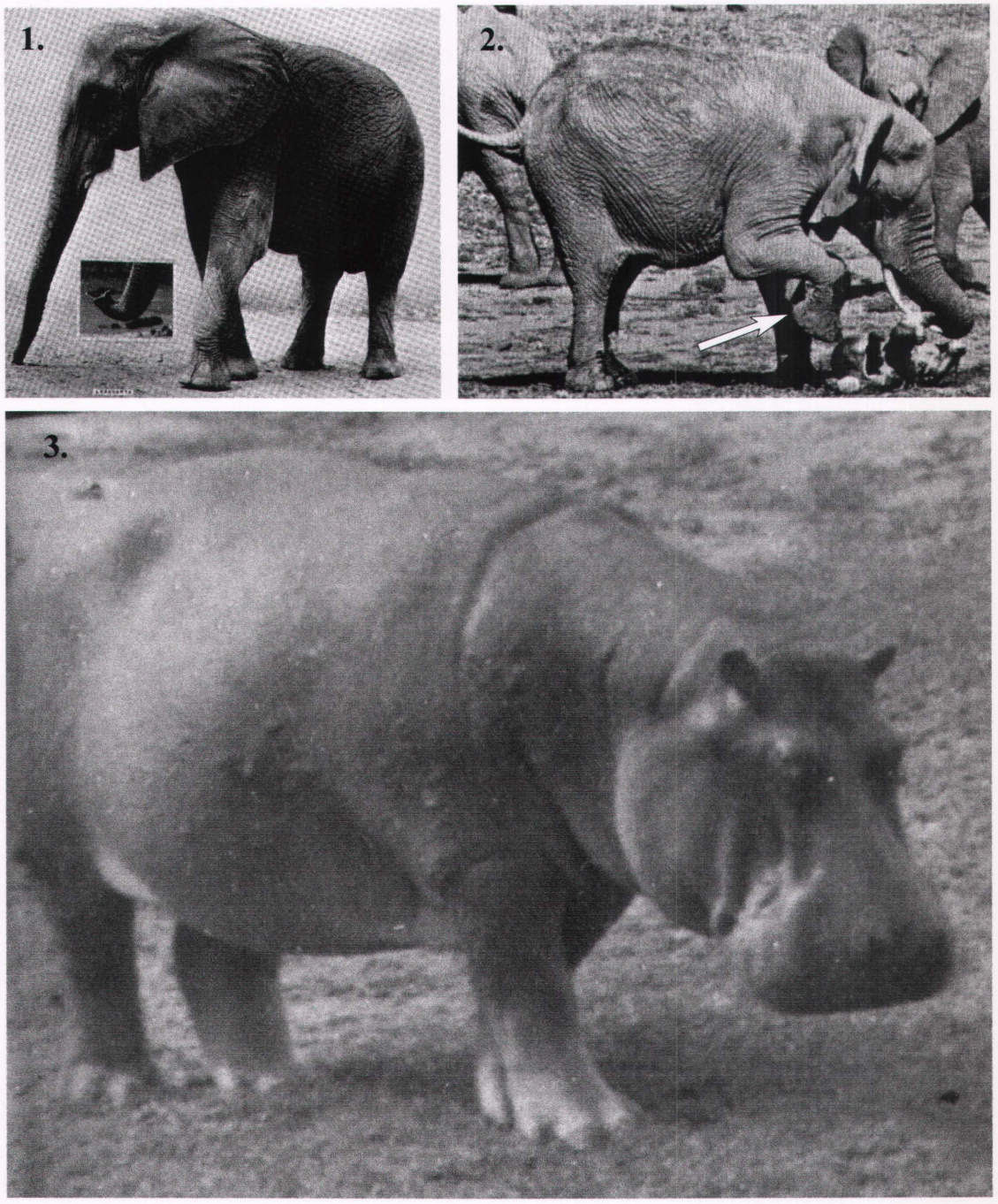


Figure 6.2.1-3: 1, The African Elephant - *Loxodonta africana* - (from Walker *et al.*, 1975). 2, *L.africana* showing fleshy pad on posterior portion of foot (Delany and Happold, 1979). 3, A hippopotamus - *Hippopotamus amphibus* - (from Eltringham, 1979).

15).

When compared with some estimates of modern animals (Alexander, 1989), the presumed *Tetrapodosaurus* footprint producer (*Sauropelta*), with all four feet in contact with the ground, distributed its weight more efficiently (49.2 kN/m2) than do domestic cattle (150 kN/m2) and elephants (70 kN/m2). However, animals have to move to get from one place to another, lifting one foot at a time (or as many as two for quadrupeds). This is taken into consideration with the dynamic loading column (Table 15). The large and medium theropods (*Irenesauripus* and *Columbosauripus*) had good reason to stay out of some of the soggy environments in which ankylosaur footprints are found. Their weight/surface area ratios are substantially higher than those of *Tetrapodosaurus*. The presumed ornithopods (*Gypsichnites*) and ornithomimids (*Irenichnites*) would have fared better than the larger theropods on muddy substrates, but perhaps their habitat preferences kept them out of the areas frequented by ankylosaurs. The ornithomimids are built for speed and probably would not sacrifice that advantage by slogging around on muddy substrates. The ornithopods likely preferred more wooded habitats in order to exercise their impressive tooth batteries on plant food that the ankylosaurs were not capable of digesting.

The observations of footprint distribution in the Smoky River Coal Mine warrant explanation. The explanation given here is capable of being tested more fully. A clearer understanding of the degree of correlation of the different tracksites along this anticline limb would be of great value, as would a more detailed sedimentological analysis. A closer look at the composition of the invertebrate ichnofaunas and a pollen analysis of each of these sites might also shed some light on the specific nature of the palaeoenvironment.

6.2 Comparison of Contemporaneous Skeletal Faunas to the Smoky River Ichnofauna

Invertebrate palaeoichnologists generally do not attempt to correlate a trace to a particular organism, recognizing that the same trace may be produced by a variety of unrelated organisms. Invertebrate traces are generally classified according to behaviour, and facies (Pemberton *et al.*, 1992). An invertebrate trace found in Cambrian rocks can have a near-exact modern analogue, even though it is certain that the organisms that made the traces were completely unrelated. As a consequence, invertebrate trace fossil studies are not preoccupied with the exact identification of the trace-maker (Sarjeant and Kennedy, 1973). However, vertebrate palaeoichnologists generally try to link ichnotaxa to analogous skeletal material (Sarjeant, 1975). Vertebrate traces do represent foot morphology so something of the anatomy of the trace-making animal is revealed (Sarjeant and Kennedy, 1973; Lockley, 1997b). The difference in position between the vertebrate and invertebrate palaeoichnologists can be attributed to the fact that a large majority of infaunal invertebrates are soft-bodied and have very little preservation potential. On the other hand, vertebrates (especially large ones) have a much better chance of being preserved.

However, even with a reasonably intact skeletal record, linking footprints to their makers is not easy. Generally, footprints can be linked with a fair degree of confidence to higher taxonomic groups and perhaps even to families (Sarjeant, 1990; Lockley, 1991). However, foot morphology is fairly conservative, so it is not considered good practice to link a particular genera to an ichnotaxon without very good reason.

The affinities of the vertebrates footprints from the Gates Formation has already been discussed. A brief comparison of some skeletal sites from the United States with an abridged faunal list will enable comparison with the Smoky River ichnofauna and their purported trace-makers.

Gates Formation (Lower Albian) Ichnotaxa and Purported Footprint-Makers

Irenesauripus	Large theropod: (*Acrocanthosaurus*)
Columbosauripus	Medium theropod: (Ornithomimid or coelurosaur)
Gypsichnites	Medium ?ornithopod: (*Tenontosaurus*)
Irenichnites	Small ornithomimid: (*Dromiceiomimus*-like)
Tetrapodosaurus	Large thyreophoran: (Nodosaurid/Ankylosaurid)

Cloverly Formation of Montana and Wyoming (Aptian-Albian)

(Occurrences taken from Weishampel, 1990; and Harris, 1998)

Large theropods:	indet. (?*Acrocanthosaurus*)
Medium theropods:	*Deinonychus*
Small theropods:	*Microvenator*
ornithomimids:	?*Ornithomimipus*
Medium ornithopods:	*Zephyrosaurus*; *Tenontosaurus*
Ankylosaurs:	*Sauropelta*
Sauropods:	?*Pleurocoelus*

Cedar Mountain Formation of Utah (Albian)

(occurrences taken from Weishampel, 1990; and Harris, 1998)

Large theropods:	?*Acrocanthosaurus*
Medium theropods:	cf. *Deinonychus*
Small theropods:	troodontid indet.
Ornithopods:	*Tenontosaurus*; ?*Iguanodon*; ?hadrosaurid
Ankylosaurs:	*Sauropelta* and others
Sauropods:	indet.

Antlers Formation of Oklahoma and Texas (Late Aptian-Middle Albian)

(occurrences taken from Weishampel, 1990)

Large theropods:	*Acrocanthosaurus*
Medium theropods:	cf. *Deinonychus* sp.
Small theropods:	troodontid indet
Ornithopods:	*Tenontosaurus*
Sauropods:	indet.

Glen Rose Formation of Texas (late Aptian-early Albian)

(occurrences taken from Weishampel, 1990)

Sauropods:	Pleurocoelus

Arundel Formation of Maryland (Aptian-Early Albian)

(occurrences taken from Weishampel, 1990 and Harris, 1998)

Large theropods:	?*Acrocanthosaurus*
Small theropods:	*Coelurus*
Ornithomimids:	?ornithomimid indet.
Ornithopods:	*Tenontosaurus*
Ankylosaurs:	Ankylosauria indet.

There are significant differences between some of the skeletal sites and the inferred fauna of the Gates Formation. For example, skeletal remains of sauropods are found in all but one of the skeletal sites, including one of the northernmost skeletal sites (Cloverly Formation of Montana). No sauropod footprints have yet been recognized from the Gates Formation or any other Lower Cretaceous tracksite in Canada. The skeletal components of the Arundel Formation of Maryland match best well with the ichnofaunal composition of the Gates Formation. The depositional environment was

that of oxbow swamps with abundant plant remains (Kranz, 1998) which is not too dissimilar to that of the Gates Formation, though the Gates had much greater development of coals.

6.3 Other Contemporaneous Vertebrate Tracksites

Gething Formation of British Columbia (Aptian): Footprints are preserved in deltaic sediments. The Peace River ichnofauna is dominated by *Amblydactylus* footprints, produced by large, bipedal hadrosaurs (Currie, 1983; 1995; Currie and Sarjeant, 1979). A wide variety of other ichnotaxa contributed to this very diverse ichnofauna, which includes dinosaurs (Sternberg, 1932; Sarjeant, 1981) , birds (Currie, 1981) and marsupial mammals (Sarjeant and Thulborn, 1986). Even though the footprints of *Tetrapodosaurus* were first discovered and characterized from a total of 14 footprints (7 manual, 7 pedal) they formed a very insignificant part of the ichnofauna.

Dakota Group of Colorado, Oklahoma and New Mexico (Late Albian - Early Cenomanian): Track-bearing beds have been estimated to have an areal extent of approximately 80,000km^2 (Lockley and Hunt, 1994). Dominated by footprints of *Caririchnium*, closely resembling *Amblydactylus* prints which are attributed to ornithopods (hadrosaurs). Also there are small, slender-toed theropods and avian *Ignotornis* footprints Lockley (1987).

Cedar Mountain Formation of Colorado (Albian): Until recently, mostly bones were found in this formation, with few footprints (Lockley and Hunt, 1994). Recent research has led to the discovery of more tracksites. The ichnofauna is dominated by ornithopods (*Caririchnium*) although the prints of theropods, sauropods and ankylosaurs are also present (Lockley *et al.*, 1999).

The Glen Rose Formation of Texas (late Aptian-early Albian): The tracksites are found in carbonate platform sequences (Lockley and Hunt, 1994). Theropod and sauropod prints (*Brontopodus*) are most common.

Discussion: Pie graphs displaying the proportions of trackways attributable to large taxonomic groups (ie. sauropoda, theropoda, ornithopoda, etc.) from Texas, Colorado, and British Columbia are constructed and presented here (Figure 6.3). From these diagrams, comparisons can be made between the different regions. It can be seen that

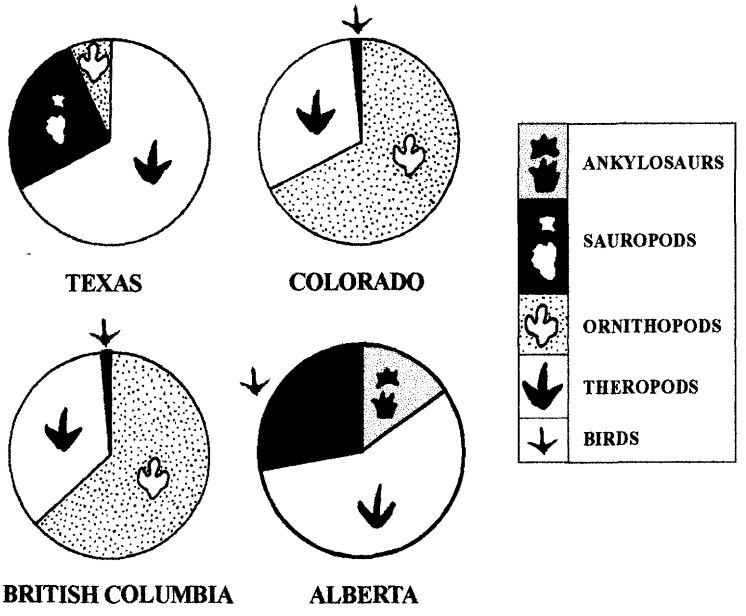


Figure 6.3. Comparison of the composition of Lower Cretaceous ichnofaunas of North America. Pie graphs for Texas, Colorado and British Columbia are from Lockley (1991).

sauropods dominated the Gulf of Mexico region in the southwest United States, along with theropods. There is only a small record of ornithopods and no ankylosaurs. In Colorado, ornithopods and theropods dominate. Canadian ichnofaunal compositions (based on the Gething Formation tracksites) appeared hitherto to be nearly identical to Colorado. The one trackway of *Tetrapodosaurus* did not even register on the graph. North America was divided into a southern region dominated by sauropods and

theropods and a northern region dominated by ornithopods and theropods. There is no physical boundary known, that would have prevented sauropods from entering higher latitudes, so it was thought that this distribution might be due to habitat preferences (Lockley, Hunt and Meyer, 1994). Almost all occurrences of *Brontopodus* (sauropod) footprints worldwide are preserved in carbonate and evaporitic facies in low latitudes, whereas ornithopod-dominated environments are characterized by "mid- and high-latitude, siliciclastic, coastal-plain [and] coal-bearing facies" (Lockley, Hunt and Meyer, 1994).

It is difficult to explain the absence of the ankylosaur tracks at many of these tracksites when their skeletal material is found in Lower Cretaceous deposits in the United States. When the Gates Formation tracksites were discovered and were found to be dominated by *Tetrapodosaurus* footprints, this shed new light on the composition of Canadian ichnofaunas. With reports of new ankylosaur tracksites worldwide (McCrea *et al.*, in press, Appendix A), it seems that the distribution of ankylosaur footprints is biased towards well-watered and well-vegetated environments. Abundant ankylosaur footprint occurrences may depend on their proximity to low energy coal swamp environments. The ankylosaur trackways in the Gates Formation are within two or three meters of a major coal seam in a low energy depositional environment. The Gething Formation is quite variable in energy (Currie, 1995), but the two *Tetrapodosaurus* trackways that Sternberg studied were located 66 m above a major coal seam, and many other recently reported ankylosaur track occurrences have been observed in coal-bearing formations (McCrea *et al.*, in press, Appendix A)

With the inclusion of trackway proportions from this study, it is easy to see that the Gates Formation ichnofauna (W3 Main) is unique to date (Figure 6.2). The vertebrate ichnofauna of Alberta, represented by prints from the W3 Main site of the Gates Formation, is dominated by theropod, bird and ankylosaur prints. However, the W3 Main site is only one of nineteen sites from the Smoky River Coal Mine. Most sites

have no other ichnotaxa besides ankylosaurs; these number in the several hundreds. The Gates ichnofauna is overwhelmingly dominated by the footprints of ankylosaurs. This is somewhat peculiar since the Gates ichnofauna is not too much younger than the Gething Formation (approximately 10 Ma) and the two sites are separated by less than 400 km. One possible explanation may be that the Gething Formation vertebrate ichnofauna was formed in a predominantly deltaic ichnofacies, while the Gates Formation vertebrate ichnofauna was formed in a coastal plain ichnofacies more closely associated with major coal seams The Gething Formation also contains economic coal seams, but tracksites have been found generally as a result of natural erosion processes throughout the sequence, whereas those of the Gates Formation are found solely as a result of the removal of one particular coal seam (Number Four).

6.4 Future Studies

The research presented here represents the first steps towards an understanding the Lower Cretaceous vertebrate ichnofauna of the Gates Formation. With the loss of the Gething Formation tracksites in the Peace River Canyon, the Gates Formation tracksites in the Smoky River Coal Mine are the best examples of large scale tracksite exposures in Canada. Unfortunately, the Gates Formation tracksites are not immune to destruction. A few have already fallen, while others have become inaccessible. The amount of time available to document any of the existing sites is limited because of the climate encountered at their altitude and proximity to the Rocky Mountains. Access to adequate resources to fund and outfit a field crew to document comprehensively the most important tracksites has yet to be achieved. The quality of the tracksites and their importance as the only substantial record of terrestrial vertebrates from the Lower Cretaceous of Canada still above water merits them far better treatment.

It is likely that new Lower Cretaceous tracksites may be recognized in western Canada. The Number Four Coal Seam is an important stratigraphic indicator of the Gates Formation

in Alberta (Langenberg *et al.*, 1987) and is actively mined in several areas, using the same mining techniques employed at the Smoky River Coal Mine. It is not unreasonable to predict that there could be several vertebrate footprint exposures in other coal mines that are either unreported or unrecognized. Since no skeletal material of terrestrial vertebrates has yet been positively identified from any "Middle" Cretaceous strata in Canada, the results of vertebrate palaeoichnology research will continue to significantly impact Canadian "Middle" Cretaceous vertebrate palaeontology. It is hoped that research on western Canadian vertebrate tracksites will continue.

6.5 Conclusions

Recent research on the vertebrate ichnofauna of the Gates Formation (Albian) near Grande Cache, Alberta has led to the identification of five ichnotaxa attributable to dinosaurs. No new dinosaur ichnotaxa were recognized although several dinosaurian ichnotaxa were emended. Emendations to *Irenesauripus mclearni* were made due to the presence of recognizable phalangeal pad impressions in some footprints. Phalangeal pad impressions were also recognized in some *Columbosauripus ungulatus* prints. Phalangeal pad impressions and terminal claw impressions were present in some specimens of *Gypsichnites pascensis*. Distinct phalangeal pad impressions were also found in some specimens of *Irenichnites gracilis*. One of the more significant emendations concerned the ichnotaxon *Tetrapodosaurus borealis*, where manual and pedal prints were found lacking any evidence of fleshy pads enclosing the digits. Some prints displayed skin impressions. Several morphotypes of *Tetrapodosaurus borealis* were recognized, due primarily to the variable consistency of the substrate that the trace-producing animals were walking upon.

Two avian ichnotaxa were recognized, one of which was a new ichnospecies (*Aquatilavipes* ichnosp. nov.). One mammalian ichnotaxon was also recognized and was described as a new ichnospecies (*Tricorynopus* ichnosp. nov.).

The majority of the research material presented herein was collected from the W3 Main tracksite within the Smoky River Coal Mine near Grande Cache, Alberta. Within the 500 m^2 study area the dominant ichnotaxon was *Aquatilavipes* ichnosp. nov., an avian ichnotaxon, however, the dinosaurian ichnotaxon *Tetrapodosaurus borealis* is the dominant ichnotaxon when all of the tracksites from this area are considered.

Observations were made of the distributions of vertebrate ichnotaxa throughout the eighteen tracksites in the Smoky River Coal Mine. There is a possibility that the distribution of ichnotaxa may reflect the habitat preference of some of the trace-producing animals. The *Tetrapodosaurus borealis* track-makers may have preferred low energy depositional settings and softer substrates with abundant plants. The other vertebrate track-makers may have preferred a slightly higher energy depositional environment, with firmer substrates.

Contemporaneous tracksites near the Gulf of Mexico are sauropod/theropod dominated while those in the mid-western states and in Canada (Peace River Canyon) are ornithopod/theropod dominated. The Smoky River ichnofauna differs markedly from all known contemporaneous North American ichnofaunas in that it is overwhelmingly dominated by the traces of ankylosaurs, with all other vertebrate ichnotaxa making up a minor component of the entire ichnofauna.

TRACKWAY LOCATION	PRINT NUMBER	FOOTPRINT LENGTH (cm)	FOOTPRINT WIDTH (cm)	DIGIT LENGTH (cm) II	III	IV	DIVARICATION II-III	III-IV	TOTAL	PACE (cm)	STRIDE (SL) (cm)	PACE ANGLE	Height (h) (m)	SL(m)/h	V min. (km/h	V avg. (km/h	V max. (km/h
	1R	49.5			49.5												
	2	48.5	40.0	36.5	48.5	32.0	39	33	72	151.5							
	3	47.5	33.5		47.5					152.0	303.5	177					
	4	47.5	38.0		47.5					147.5	299.5*	161					
D1-I9	5	47.0	35.5		47.0					161.5	307.5	168					
	6	47.0	38.5		47.0					152.5	313.0	168					
	7	48.0	38.0		48.0					154.5	305.0	167	2.40	1.27	6.30	6.52	6.80
x̄		**47.9**	**37.3**	**36.5**	**47.9**	**32.0**	**39**	**33**	**72**	**153.3**	**305.7**	**168**	**2.40**	**1.27**	**6.30**	**6.52**	**6.80**
	1L																
	2	44.0	42.0		44.0					160.0							
	3	47.5	41.0		47.5					140.0	296.5	160					
G6-bb6	4	43.0	41.5		43.0					158.5	297.4	167					
	5	46.0	44.0	36.5	46.0	33.5	36	42	78	155.0	310.5*	162					
	6									158.5	306.0	156	2.28	1.33	6.59	6.84	7.24
x̄		**45.1**	**42.1**	**36.5**	**45.1**	**33.5**	**36**	**42**	**78**	**154.4**	**302.6**	**161**	**2.28**	**1.33**	**6.59**	**6.84**	**7.24**

Table 1. Measurements of *Irenesauripus mclearni* footprints and trackways from the W3 Main site, Smoky River Coal Mine, Alberta.

+ High

✖ Low

Data Source For Measurements † Data taken from text figure	FOOTPRINT LENGTH (cm)	FOOTPRINT WIDTH (cm)	DIGIT LENGTH (cm) II	III	IV	DIVARICATION II-III	III-IV	TOTAL	PACE (avg.) (cm)	STRIDE (SL) (cm)	PACE ANGLE
Irenesauripus mclearni Peace River (Sternberg, 1932)	38.0	31.8	29.2	38.0	28.0	37°	33°	70°	94.0	144.0†	134°†
Irenesauripus acutus Peace River (Sternberg, 1932)	53.5	40.0	40.5	53.5	41.5	18°	40°	58°	173.0		

Table 2. Comparison between *Irenesauripus mclearni* and *I. acutus* from the Gething Formation (Aptian) of the Peace River Canyon, British Columbia. Measurements are from holotypes of each ichnotaxon (Sternberg, 1932).

TRACKWAY LOCATION	PRINT NUMBER	FOOTPRINT LENGTH (cm)	FOOTPRINT WIDTH (cm)	DIGIT LENGTH (cm) II	III	IV	DIVARICATION II-III	III-IV	TOTAL	PACE (cm)	STRIDE (SL) (cm)	PACE ANGLE	Height (h) (m)	SL(m)/h	V min. (km/h	V avg. (km/h	V max. (km/h
	1L		22.5														
cc16-gg15	2	25.0	22.5	16.5	25.0	18.8	41	46	87	136.5							
	3	28.0	25.5		28.0					128.0	264.0	170	1.39	1.90		9.68	
x̄		**26.5**	**23.5**	**16.5**	**26.5**	**18.8**	**41**	**46**	**87**	**132.3**	**264.0**	**170**	**1.39**	**1.90**		**9.68**	
	1R	22.0	18.0		22.0												
A10-aa9	2	25.0	18.5		25.0					103.5							
	3	24.5	18.5	19.0	24.5	21.0	33	32	65	101.0	201.5	158	1.14	1.77		9.00	
x̄		**23.8**	**18.3**	**19.0**	**23.8**	**21.0**	**33**	**32**	**65**	**102.3**	**201.5**	**158**	**1.14**	**1.77**		**9.00**	
	1R	22.0	24.0	18.0	22.0	19.5	51	38	89								
B27-D27	2	24.0	24.0		24.0					100.0							
	3	23.0	26.0		23.0					108.0	208.3	167	1.09	1.91		8.65	
x̄		**23.0**	**24.7**	**18.0**	**23.0**	**19.5**	**51**	**38**	**89**	**104.0**	**208.3**	**167**	**1.09**	**1.91**		**8.65**	
	1R	26.5	24.0		26.5												
C26-C28	2	26.0	26.5	23.0	26.0	19.0	37	48	85	117.0							
	3	26.0			26.0					120.0	236.5	168	1.44	1.64		7.78	
x̄		**26.2**	**25.3**	**23.0**	**26.0**	**19.0**	**37**	**48**	**85**	**118.5**	**236.5**	**168**	**1.44**	**1.64**		**7.78**	
	1L		24.5														
G23-E23	2	26.0	24.0		26.0					110.0							
	3	26.5	25.5	23.0	26.5	19.5	39	39	78	107.5	217.0	169	1.43	1.52		6.77	
x̄		**26.3**	**24.7**	**23.0**	**26.3**	**19.5**	**39**	**39**	**78**	**108.8**	**217.0**	**169**	**1.43**	**1.52**		**6.77**	

Table 3. Measurements of *Columbosauripus ungulatus* footprints and trackways from the W3 Main site, Smoky River Coal Mine, Alberta.

TRACKWAY LOCATION	PRINT NUMBER (cm)	FOOTPRINT LENGTH (cm)	FOOTPRINT WIDTH (cm)	DIGIT LENGTH (cm) II	III	IV	DIVARICATION II-III	III-IV	TOTAL	PACE (cm)	STRIDE (SL) (cm)	PACE ANGLE	Height (h) (m)	SL(m)/h	V min. (km/h	V avg. (km/h	V max. (km/h
	1	20.5	17.0		20.5												
aa5-E8	2	20.5	18.5	16.7	20.5	16.5	33	31	64	96.0							
	3	20.5	17.5		20.5					95.5	190.5	171					
	4									88.0	182.0	171					
	5	21.0	18.0		21.0					99.5	186.0	168					
	6	20.5	17.5		20.5					91.5	191.0+	177					
	7	21.0	18.0		21.0					92.0	181.0×	166	.968	1.92	7.88	8.24	8.60
x̄		**20.7**	**17.8**	**16.7**	**20.7**	**16.5**	**33**	**31**	**64**	**93.8**	**186.1**	**171**	**.968**	**1.92**	**7.88**	**8.24**	**8.60**
bb17-bb16	1	24.5	20.5		24.5												
	2	25.0	20.5		25.0				67	124.0			1.190				
x̄		**24.8**	**20.5**		**24.8**				**67**	**124.0**			**1.190**				
	1L	18.0	14.0		18.0												
	2	19.0	15.0		19.0					86.5							
cc8-E2	3	19.5	17.0		19.5					91.5	178.5×	174					
	4	20.0	16.0		20.0					120.0	212.0	179					
	5	19.5	14.5		19.5					129.0	248.0	169					
	6	20.0	15.5		20.0					140.5	270.0	180					
	7	20.0	14.5		20.0					137.0	277.5+	169					
	8	20.0	16.0		20.0					140.0	270.8	179					
	9	19.5	17.5	13.5	19.5	15.0	34	42	76	137.0	277.0	173	.904	2.74	8.35	14.4	17.4
x̄		**19.5**	**15.6**	**13.5**	**19.5**	**15.0**	**34**	**42**	**76**	**122.7**	**247.7**	**175**	**.904**	**2.74**	**8.35**	**14.4**	**17.4**
	1																
hh11-ii13	2	24.5	16.1	19.5	24.5	17.9	23	28	51	112.6	219.1	175					
	3									107.0			1.170	1.87		8.71	
x̄		**24.5**	**16.1**	**19.5**	**24.5**	**17.9**	**23**	**28**	**51**	**109.8**	**219.1**	**175**	**1.170**	**1.87**		**8.71**	
	1L																
	2									105.0							
B4-aa8	3	25.5	17.0	20.0	25.5	19.0	23	27	50	102.5	206.5+	172					
	4									103.5	206.0×	180					
	5									103.5	206.0	167	1.238	1.67	7.34	7.38	7.42
x̄		**25.5**	**17.0**	**20.0**	**25.5**	**19.0**	**23**	**27**	**50**	**103.6**	**206.2**	**173**	**1.238**	**1.67**	**7.34**	**7.38**	**7.42**

Table 4a. Measurements of *Gypsichnites pascensis* footprints and trackways from the W3 Main site, Smoky River Coal Mine, Alberta.

+ high
× low

TRACKWAY LOCATION	PRINT NUMBER (cm)	FOOTPRINT LENGTH (cm)	FOOTPRINT WIDTH (cm)	DIGIT LENGTH (cm) II	III	IV	DIVARICATION II-III	III-IV	TOTAL	PACE (cm)	STRIDE (SL) (cm)	PACE ANGLE	Height (h) (m)	SL(m)/h	V min. (km/h	V avg. (km/h	V max. (km/h
D9-C1	1L	22.0	21.0		22.0												
	2	28.0	21.0		28.0					111.0							
	3	26.0	21.5		26.0					108.5	202.0×	174					
	4	26.0	21.0	21.5	26.0	22.5	30	26	56	113.0	202.0	178					
	5	23.0	21.0		23.0					112.0	225.0+	180					
	6	26.0	19.5		26.0					108.5	220.0	179					
	7	25.0	21.0		25.0					109.0	217.0	174					
	8		17.0							114.0	202.5	179	1.206	1.75	7.27	7.86	8.71
$\bar{x}$		**25.1**	**20.4**	**21.5**	**25.1**	**22.5**	**30**	**26**	**56**	**110.9**	**211.4**	**177**	**1.206**	**1.75**	**7.27**	**7.86**	**8.71**
E26-F24	1R	19.0	16.5	14.0	19.0	14.0	39	33	72								
	2	19.5	17.5		19.5					114.5							
	3	17.0	17.5		17.0					112.5	227.0	177					
	4												0.852	2.66		13.32	
$\bar{x}$		**18.5**	**17.2**	**14.0**	**18.5**	**14.0**	**39**	**33**	**72**	**113.5**	**227.0**	**177**	**0.852**	**2.66**		**13.32**	
F2-aa4	1L	23.5	22.0		23.5												
	2	25.0	23.5		25.0					123.0							
	3	23.0	22.0		23.0					123.0	245.0	175					
	4	23.5	22.0	19.5	23.5	19.5	35	35	70	124.5	242.0	157					
	5	22.0	22.0		22.0					125.0	249.0+	179					
	6	25.0	22.0		25.0					107.5	217.5	136					
	7	23.0	22.0		23.0					84.8	191.0×	170					
	8	25.0	22.0		25.0					122.0	205.5	170	1.135	1.98	7.13	9.40	11.12
$\bar{x}$		**23.8**	**22.2**	**19.5**	**23.8**	**19.5**	**35**	**35**	**70**	**115.7**	**225.0**	**164.5**	**1.135**	**1.98**	**7.13**	**9.40**	**11.12**
G22-D18	1R	21.0	16.5		21.0												
	2	21.0	17.0	16.5	21.0	15.5	33	29	62	112.0							
	3									117.0	227.5×	177					
	4	21.0	17.0		21.0					113.5	230.0	177					
	5	20.0	16.5		20.0					117.0	231.0	177					
	6	21.0	18.0		21.0					115.5	233.0+	178	0.973	2.37	11.48	11.70	11.92
$\bar{x}$		**20.8**	**17.0**	**16.5**	**20.8**	**15.5**	**33**	**29**	**62**	**115.0**	**230.4**	**177**	**0.973**	**2.37**	**11.48**	**11.70**	**11.92**

Table 4b. Measurements of *Gypsichnites pascensis* footprints and trackways from the W3 Main site, Smoky River Coal Mine, Alberta.

+ high
× low

TRACKWAY LOCATION	PRINT NUMBER	FOOTPRINT LENGTH (cm)	FOOTPRINT WIDTH (cm)	DIGIT LENGTH (cm) II	III	IV	DIVARICATION II-III	III-IV	TOTAL	PACE (cm)	STRIDE (SL) (cm)	PACE ANGLE	Height (h) (m)	SL(m)/h	V min. (km/h	V avg. (km/h	V max. (km/h
	1L	24.5	22.0		24.5												
	2	28.8	23.0		28.8					118.0							
	3																
	4										240.0	175					
H11-bb2	5	26.0	21.5		26.0					180.0							
	6	29.0	24.0	13.5	29.0	25.0	37	27	64	118.5	239.0	178					
	7	26.5	22.5		26.5					120.5	242.0*						
	8	29.0	25.0		29.0					114.0	234.5	179					
	9	25.0	22.0		25.0					119.0	233.0	178					
	10	25.0	21.5		25.0					121.5	241.0	176					
	11	29.0	26.0		29.0					114.0	235.5	175					
	12	28.0	21.5		28.0					115.5	229.5*	177	1.316	1.80	8.17	8.60	8.75
x̄		**27.1**	**22.9**	**13.5**	**27.1**	**25.0**	**37**	**27**	**64**	**124.6**	**236.8**	**177**	**1.316**	**1.80**	**8.17**	**8.60**	**8.75**

Table 4c. Measurements of *Gypsichnites pascensis* footprints and trackways from the W3 Main site, Smoky River Coal Mine, Alberta.

TRACKWAY LOCATION	PRINT NUMBER	FOOTPRINT LENGTH (cm)	FOOTPRINT WIDTH (cm)	DIGIT LENGTH (cm) II	III	IV	DIVARICATION II-III	III-IV	TOTAL	PACE (cm)	STRIDE (SL) (cm)	PACE ANGLE	Height (h) (m)	SL(m)/h	V min. (km/h	V avg. (km/h	V max. (km/h
	1L	25.0	18.0		25.0												
	2	23.0	18.5		23.0					101.0							
	3	22.0	17.0		22.0					99.0	200.5	180					
	4	23.0	19.0		23.0					98.5	196.0	165					
	5	23.0	16.0		23.0					101.0	199.5	176					
	6	23.0	20.0		23.0					98.5	199.5	173					
	7	21.0	18.5	12.5	21.0	15.0	32	31	63	96.0	194.5	177					
	8	24.0	19.0		24.0					97.5	193.5	176					
	9	23.0	19.5		23.0					105.5	202.5	178					
J8-E26	10	23.5	20.0		23.5					97.0	202.0	177					
	11																
	12																
	13	24.0	18.0		24.0												
	14																
	15	23.5	18.0		23.5						208.5						
	16	24.0	21.0		24.0					97.5							
	17	23.0	20.0		23.0					105.5	203.0	176					
	18	22.0	18.5		22.0					109.0	215.0+	178					
	19	21.5	20.0		21.5					103.5	212.5	176					
	20	23.0	17.5	17.5	23.0		31	27	58	107.5	109.5×	171	1.092	1.79	2.95	7.74	9.11
x̄		**23.0**	**18.7**	**15.0**	**23.0**	**15.0**	**32**	**29**	**61**	**101.2**	**195.1**	**175**	**1.092**	**1.79**	**2.95**	**7.74**	**9.11**

Table 4d. Measurements of *Gypsichnites pascensis* footprints and trackways from the W3 Main site, Smoky River Coal Mine, Alberta.

+ high
× low

TRACKWAY LOCATION	PRINT NUMBER	FOOTPRINT LENGTH (cm)	FOOTPRINT WIDTH (cm)	DIGIT LENGTH (cm) II	III	IV	DIVARICATION II-III	III-IV	TOTAL	PACE (cm)	STRIDE (SL) (cm)	PACE ANGLE	Height (h) (m)	SL(m)/h	V min. (km/h	V avg. (km/h	V max. (km/h
	1R	16.5	14.0		16.5												
	2	16.0	13.2		16.0					106.0							
aa21-C18	3	13.5	12.0		13.5					108.5	214.5×						
	4	15.0	12.0		15.0				65	106.5	215.0						
	5	14.5	11.5	8.0	14.5	8.0	44	39	83	112.5	219.0+		.841	2.57	12.3	12.4	12.7
x̄		**15.1**	**12.5**	**8.0**	**15.1**	**8.0**	**44**	**39**	**74**	**108.4**	**216.2**		**.841**	**2.57**	**12.3**	**12.4**	**12.7**
	1L	17.0	15.5		17.0												
	2	19.0	14.5		19.0					69.5							
	3	17.5	15.0		17.5					82.0	151.5	180					
bb20-B22	4	17.0	15.0	13.5	17.0	14.5	38	30	68	75.0	155.0+	163					
	5	17.5	15.5		17.5					73.0	148.5	178					
	6	17.0	14.5		17.0					71.5	144.0×	173	.978	1.53	5.33	5.72	6.05
x̄		**17.5**	**15.0**	**13.5**	**17.5**	**14.5**	**38**	**30**	**68**	**74.2**	**149.8**	**174**	**.978**	**1.53**	**5.33**	**5.72**	**6.05**

Table 5. Measurements of *Irenichnites gracilis* footprints and trackways from the W3 Main site, Smoky River Coal Mine, Alberta.

+ High

× Low

TRACKWAY LOCATION	PRINT NUMBER	FOOTPRINT LENGTH (cm)	FOOTPRINT WIDTH (cm)	DIGIT LENGTH (cm) I	II	III	IV	DIVARICATION I-II	II-III	III-IV	TOTAL	PACE (cm)	STRIDE (SL) (cm)	PACE ANGLE	Height (h) (m)	SL(m)/h	V min. (km/h)	V avg. (km/h)	V max. (km/h)
aa23-H25	1L	51.0	46.0																
	2											94.5							
	3											90.0	143.5*	101					
	4											112.0	158.0	101					
	5											103.0	178.5+	110					
	6											112.0	175.5	98					
	7											98.5	163.0	99					
	8											116.0	163.0	97					
	9											97.5	168.0	102					
	10											107.5	166.5	107					
	11	53.0	46.0									91.5	160.5	107	2.08	0.79	2.20	2.74	3.13
$\bar{x}$		**52.0**	**46.0**									**102.3**	**164.1**	**102**	**2.08**	**0.79**	**2.20**	**2.74**	**3.13**
B20-B16	1L		36.0																
	2											84.0	129.5*						
	3																		
	4	40.0	40.0	34.5	39.0	40.0	35.1	23	27	22	72	88.5	155.5+						
	5											91.5							
	6													120	1.60	0.89	2.48	2.95	3.38
$\bar{x}$		**40.0**	**38.0**	**34.5**	**39.0**	**40.0**	**35.1**	**23**	**27**	**22**	**72**	**88.0**	**142.5**	**120**	**1.60**	**0.89**	**2.48**	**2.95**	**3.38**
G12-H7	1L																		
	2											103.0							
	3											93.0	158.0	110					
	4											97.4	147.5	110					
	5											111.5	155.0	105					
	6											111.2	162.1	110					
	7											107.5	158.8	105					
$\bar{x}$												**103.9**	**156.3**	**108**					

Table 6a. Measurements of *Tetrapodosaurus borealis* footprints and trackways from the W3 Main site, Smoky River Coal Mine, Alberta.

+ High

✖ Low

TRACKWAY LOCATION	PRINT NUMBER	FOOTPRINT LENGTH (cm)	FOOTPRINT WIDTH (cm)	DIGIT LENGTH (cm) I	II	III	IV	DIVARICATION I-II	II-III	III-IV	TOTAL	PACE (cm)	STRIDE (SL) (cm)	PACE ANGLE	Height (h) (m)	SL(m)/h	V min. (km/h)	V avg. (km/h)	V max. (km/h)
H17-L24	1L																		
	2											111.0							
	3											80.0	159.0	111					
	4											122.0	166.0	109					
	5											79.0	163.0	105					
	6											104.5	138.0	97					
	7											99.0	160.0	102					
	8											91.0	161.0	117					
	9											99.0	152.0	105					
	10											103.0	165.0	113					
	11											100.0	172.0	115					
	12											95.5	160.0	110					
$\bar{x}$												**99.5**	**159.6**	**108**					
L14-L16	1L																		
	2											97.0							
	3											98.9	157.5	112					
$\bar{x}$												**98.0**	**157.5**	**112**					

Table 6b. Measurements of *Tetrapodosaurus borealis* footprints and trackways from the W3 Main site, Smoky River Coal Mine, Alberta.

+ High

✖ Low

Specimen Number		Digit Length (cm)					Divarication (cm)				
		I	II	III	IV	V	I-II	II-III	III-IV	IV-V	TOTAL
TMP 98.89.2	manus	12.0	9.5	10.0	8.0	10.0	25	21	26	38	110
	pes	10.0	12.5	12.5	16		20	25	29		74
TMP 98.89.4	manus	6.0	6.0	10.0	9.0	8.5	41	51	58	56	202
	pes	15.0	14.5	14.0	12.5		27	26	26		79
TMP 99.49.2	manus	13.0	7.5	6.5	5.0	4-*	60	58	48	34	200

Table 6c. Measurements of *Tetrapodosaurus* prints (manus and pes). Digit length measurements are taken down the long axis of the digits to the hypex to demonstrate a lack of enclosing flesh. Note * = incomplete digit.

TRACKWAY LOCATION	PRINT NUMBER	FOOTPRINT LENGTH (cm)	FOOTPRINT WIDTH (cm)	PACE (cm)	STRIDE (SL) (cm)	Height (h) (m)	SL(m)/h	V min. (km/h)	V avg. (km/h)	V max. (km/h)
Manus	1L	24.0	37.8							
	2	28.9	48.9	85.8						
	3	24.8	46.9	107.6	129.0					
	4	23.5	36.5	77.0	144.0					
	5	22.5	45.8	91.6	139.0					
	6	17.2	34.5	88.6	136.8					
	7	22.0	35.2	93.0	142.5					
	8	24.0	35.5	77.5	135.5					
	9	25.0	34.2	95.5	125.0					
$\bar{x}$		23.5	39.5	79.6	105.8					
Pes	1	28.2	47.2							
	2	40.0	52.0	87.3						
	3	28.5	48.0	78.8	142.0					
	4	28.9	47.5	81.9	142.5+					
	5	34.0	36.7	79.5	138.5					
	6	29.5	42.6	76.9	140.4					
	7	30.2	46.4	73.0	135.0					
	8	30.0	43.0	71.2	124.0×	124.8	1.09	3.11	3.68	3.92
$\bar{x}$		**31.2**	**45.4**	**78.4**	**137.1**	**124.8**	**1.09**	**3.11**	**3.68**	**3.92**

Table 7. Measurements of *Tetrapodosaurus borealis* footprints and trackways from the 12 Mine South, A-Pit site, Smoky River Coal Mine, Alberta.

+ High
× Low

SPECIMEN NUMBER	PRINT NUMBER	FOOTPRINT LENGTH (mm)	FOOTPRINT WIDTH (mm)	DIGIT LENGTH (mm)			DIVARICATION		
				II	III	IV	II-III	III-IV	TOTAL
NATURAL CAST BLOCK TMP 98.89.21	A	47	55	34	47	32	46	62	108
	B	44	57	42	44	38	42	48	90
	C	42	33	32	42	30	37	34	71
	D	32	37	25	32	27	55	43	98
	E	31	43	23	31	24	77	53	130
	F	35	35	26	35	26	47	48	95
NATURAL MOULD BLOCK TMP 98.89.20	A	53	69	43	53	38	58	68	126
	B	45	63	34	45	38	61	71	132
	C	33	45	24	33	33	53	52	105
	D		49	28		28	68	66	134
	E	25	31	19	25	20	53	52	105
	F		40						
	G			40			61	62	123
TMP 90.30.1	A	40	55	33	40	27	75	63	138
	B	37	57	26	37	35	84	61	145
	C	41	55	29	41	32	64	74	138
TMP 79.23.3 and BCPM 744	76	38	47	22	34	24	48	70	118

Table 8. Measurements of *Aquatilavipes swiboldae* footprints and trackways from the W3 Main site (TMP 98.89.20 and TMP 98.89.21), Smoky River Coal Mine, Alberta; Highway 40 site (TMP 90.30.1) near the entrance to the Smoky River Coal Mine; and Peace River Canyon (TMP 79.23.37 and BCPM 744).

TRACKWAY LOCATION	PRINT NUMBER	FOOTPRINT LENGTH (mm)	FOOTPRINT WIDTH (mm)	DIGIT LENGTH (mm) II	III	IV	DIVARICATION II-III	III-IV	TOTAL	PACE (mm)	STRIDE (mm)	PACE ANGLE
aa6 - aa7	1(R)	77	112									
	2	85	115							240		150
	3	80	105							219	445	153
	4	65	110							248	450	157
	5	70	95							230	462	158
	6	65	105	55	65	62	68	54	122	235	455	159
	7	68	95							252	479	151
	8	72	87							240	473	
$\bar{X}$		73	100	55	65	62	68	54	122	238	461	155
cc18 - dd18	1(R)	70	101	60	70	55	50	70	120			
	2	68	107							220		135
	3	76	95							180	365	150
	4	67	108							235	405	
$\bar{X}$		70	103	60	70	55	50	70	120	212	385	143
A9	1(L)	90	110	77	90	68	50	60	110	230		
	2	80	108									
$\bar{X}$		85	109	77	90	68	50	60	110	230		
B4 - B5	1(R)	64	94	52	64	56	72	63	135			
	2	73	94							261		163
	3	72	77							261	514	178
	4	70	86							254	514	
$\bar{X}$		70	88	52	64	56	72	63	135	257	514	171
F3	1(L)	95	107									
	2	85	100							220		140
	3	90	110	71	90	67	55	69	124	210	410	132
	4	87	115							250	420	
$\bar{X}$		89	108	71	90	67	55	69	124	227	415	136
G5 - F6	1(L)	78	99									
	2	81	100							218		127
	3	78	102							225	396	144
	4	75	104	58	75	55	67	65	132	220	423	149
	5	80	96							225	432	153
	6	82	110							229	442	
$\bar{X}$		79	102	58	75	55	67	65	132	223	423	143
G18 - F19	1(L)	70	103									
	2	75	103	68	75	65	60	65	125	230		165
	3	72	102							235	460	140
	4	74								190	390	147
	5	74	106							270	430	151
	6	72								225	480	151
	7	76								315	530	
$\bar{X}$		73	104	68	75	65	60	65	125	244	458	143
H20 - H19	1(L)	63										
	2	75								300		166
	3	70	115	60	70	65	62	59	131	305	600	172
	4	80								260	570	
$\bar{X}$		72	115	60	70	65	62	59	131	288	585	169

Table 9a. Measurements of *Aquatilavipes* ichnosp. nov. footprints and trackways from the W3 Main site, Smoky River Coal Mine, Alberta.

TRACKWAY LOCATION	PRINT NUMBER	FOOTPRINT LENGTH (mm)	FOOTPRINT WIDTH (mm)	DIGIT LENGTH (mm) II	III	IV	DIVARICATION II-III	III-IV	TOTAL	PACE (mm)	STRIDE (mm)	PACE ANGLE	FOOTPRINT ROTATION
TRACKWAY A PARATYPE SLAB	1(R)	90	120	73	90	67	50	69	119				+30
	2	83	126	79	83	60	52	82	134	208		156	-4
	3	95	110	55	95	62	63	74	137	273	476	156	+22
	4	101	116	62	101	71	58	68	126	227	489	159	+35
	5	89	116	68	89	67	54	70	124	215	433	163	+14
	6	88	119	65	88	74	61	58	119	215			+23
	7	88	117	68	88	69	58	61	119	221	452		+25
	8												+19
	9	80	123	67	80	69	61	67	128				
	10	89			89	60	55	76	131	234			+41
$\bar{X}$		89	118	67	89	67	57	69	126	463	463	159	23
TRACKWAY B PARATYPE SLAB	1(R)	85	107	54	85	60	71	79	150				
	2												
	3	83	108	60	83	69	58	55	113		510		+30
	4	82	99	55	82	63	61	53	114	248			+16
	5	85	111	61	85	66	64	55	119	237	476	158	+24
	6												-30
	7	88	95	56	88	64	50	57	107		525		+16
	8	80	110	71	80	67	44	52	96	298			0
	9	88	116	71	80	67	84	53	137	214	510	173	+27
$\bar{X}$		84	107	61	83	65	62	58	119	249	505	166	14

Table 9b. Measurements of *Aquatilavipes* ichnosp. nov. footprints and trackways from the W3 Main site, Smoky River Coal Mine, Alberta. Note: + = footprint pointing toward midline of trackway, - = footprint pointing outward from midline of trackway.

Ichnotaxa	Bedding Planes A	B	C	TOTAL
***Tetrapodosaurus* ichnosp.**	98	46	65	209
***Irenesauripus* ichnosp.**	6	0	13	19
Columbosauripus ichnosp.	44	13	4	61
***Gypsichnites* ichnosp.**	4	66	106	176
***Irenichnites* ichnosp.**	17	1	2	20
***Aquatilavipes* ichnosp. nov.**	1	550	191	742
***A.* ichnosp. idet.**	0	2	0	2
TOTAL	170	678	381	1229

Table 10. Footprint proportions of vertebrate ichnotaxa at the W3 Main site (grid area only).

Ichnotaxa	Bedding Planes			TOTAL
	A	B	C	
***Tetrapodosaurus* ichnosp.**	4	2	5	11
***Irenesauripus* ichnosp.**	1	0	2	3
***Columbosauripus* ichnosp.**	11	3	0	14
***Gypsichnites* ichnosp.**	1	9	11	21
***Irenichnites* ichnosp.**	2	0	1	3
***Aquatilavipes* ichnosp. nov.**	0	15	5	20
***A.* ichnosp. idet.**	0	0	0	0
TOTAL	19	29	24	72

Table 11. Trackway proportions of vertebrate ichnotaxa at the W3 Main site (grid area only).

Irenesauripus mclearni			*Gypsichnites pascensis*			*Aquatilavipes ichosp.nov.*		
Location	Bearing	# Prints	Location	Bearing	# Prints	Location	Bearing	# Prints
H1-L6	55°	6	D16-C15	244°	2			(1)*
		(6)*			(4)*			

Columbosauripus ungulatus			*Tetrapodosaurus borealis*			*Irenichnites gracilis*		
Location	Bearing	# Prints	Location	Bearing	# Prints	Location	Bearing	# Prints
K6-K12	84°	4	aa23-H25	16°	22	aa20-C18	316°	5
I0-L4	54°	2	F26-aa16	249°	29	bb19-B22	22°	6
L18-J16	230°	2	D28-B16	257°	12			(17)*
J21-I17	258°	3	H17-M24	52°	24			
K19-J18	214°	2			(98)*			
K20-J19	201°	2						
K24-H21	221°	2						
H24-G23	262°	2						
C16-C28	90°	5						
B26-D27	23°	2						
B27-C28	48°	2						
		(44)*						

Table 12. W3 Main site: A-level trackway bearings. * Total number of footprints of the ichnotaxon on this bedding plane. Includes solitary footprints as well as those making up a trackway.

Tetrapodosaurus borealis			*Aquatilavipes* ichnogen. indet.			*Irenichnites gracilis*		
Location	Bearing	# Prints	Location	Bearing	# Prints	Location	Bearing	# Prints
J7-aa14	142	20			(2)*			(1)*
E17-G20	53	10						
		(46)*						

Aquatilavipes ichnosp. nov.			*Gypsichnites pascensis*			*Columbosauripus ungulatus*		
Location	**Bearing**	**# Prints**	**Location**	**Bearing**	**# Prints**	**Location**	**Bearing**	**# Prints**
F1-F1	299	2	J7-E26	115	17	A10-aa9	256	3
I1-J1	321	3	J1-J3	90	2	F24-F26	94	2
L2-K2	225	3	H6-M1	318	6	G23-E23	181	3
K2-K2	181	4	I8-K10	42	3			(13)*
M2-L2	207	3	H12-I15	71	3			
G3-H3	167	6	G22-D17	238	6			
J4-K4	348	4	F21-D18	238	6			
K13-K13	153	3	bb17-bb16	275	2			
I14-H14	178	4	E26-F24	310	3			
G16-I15	356	8			(66)*			
G16-H16	5	5						
G18-F19	148	7						
D18-E18	358	5						
cc18-dd18	178	4						
D20-D20	171	3						
		(550)*						

Table 13. W3 Main site: B-level trackway bearings. * Total number of footprints of the ichnotaxon on this bedding plane. Includes solitary footprints as well as those making up a trackway.

Irenesauripus mclearni			*Columbosauripus ungulatus*			*Irenichnites gracilis*		
Location	Bearing	# Prints	Location	Bearing	# Prints	Location	Bearing	# Prints
D1-I9	56°	7			(4)*	F16-G16	344°	2
G6-bb6	177°	6						(2)*
		(13)*						

Gypsichnites pascensis			*Tetrapodosaurus borealis*			*Aquatilavipes ichnosp. nov.*		
Location	**Bearing**	**# Prints**	**Location**	**Bearing**	**# Prints**	**Location**	**Bearing**	**# Prints**
dd8-E2	315°	9	bb1-A4	58°	8	aa6-aa7	91°	8
aa5-E8	33°	7	cc2-aa13	79°	15	B4-B4	90°	3
F2-aa2	147-227°	8	D2-G4	50°	10	G5-H6	160°	6
H11-bb2	226°	11	F9-G6	279°	10	G10-G10	167°	5
E9-C1	263°	8	G15-H7	281°	13	G13-G13	338°	3
B4-A8	104°	5			(65)*			(191)*
D5-F7	58°	3						
F13-G10	295°	4						
A14-A13	269°	2						
E16-E14	265°	2						
F10-H10	337°	2						
		(106)*						

Table 14. W3 Main site: C-level trackway bearings. * Total number of footprints of the ichnotaxon on this bedding plane. Includes solitary footprints as well as those making up a trackway.

Ichnotaxon	Surface Area (m^2) Manus	Pes	Trackmaker	Mass Estimate (kg)	Weight Estimate kN	Weight/Area kN/m^2	Dynamic Loading
Tetrapodosaurus	0.105	0.210	*Sauropelta*	3100	31	49.2	**(2 manus, 2 pes)**
						59.0	**(1 manus, 2 pes)**
						73.8	**(2 manus, 1 pes)**
						98.4	**(1 manus, 1 pes)**
Irenesauripus		0.120	*Acrocanthosaurus*	2300	23	95.8	**(2 pes)**
						191.7	**(1 pes)**
Columbosauripus		0.063	Medium Theropod	750	7.5	59.5	**(2 pes)**
						119.0	**(1 pes)**
Gypsichnites		0.077	*Tenontosaurus?*	500	5.0	32.5	**(2 pes)**
						64.9	**(1 pes)**
Ireichnites		0.039	*Dromiceiomimus*-like	144	1.44	18.5	**(2 pes)**
						36.9	**(1 pes)**

Table 15. Comparative weight and surface area calculations for dinosaurian taxa thought to be responsible for producing the footprints seen from the Gates Formation in the Smoky River Coal Mine, Alberta. Mass estimates are from Damuth (1994); procedure for calculations of mass and mass/surface area from Alexander (1989); surface area of footprints taken directly from footprint illustrations: *Irenesauripus* (Figure 4.1.1); *Columbosauripus* (Figure 4.4.1); *Gypsichnites* (Figure 4.5.2), *Irenichnites* (Figure 4.7.1)

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APPENDIX A

GLOBAL DISTRIBUTION OF PURPORTED ANKYLOSAUR TRACK OCCURRENCES

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Note: During a visit to the University of Colorado at Denver in February, 1997, Dr. Lockley invited me to co-author a manuscript he had started, which was a survey of known ankylosaur tracksites (there were not very many known at that time). Within a year, as a result of my research in the Smoky River Coal Mine, Alberta and a desire to help a budding vertebrate palaeoichnologist, Dr. Lockley asked me to take over the primary author responsibilities for the ankylosaur manuscript. We were soon joined by Dr. C.A. Meyer (Switzerland), primarily for the treatment of the Bolivian material.

For the purpose of including this manuscript in the Appendix of this thesis, Dr. Lockley and I have agreed that my estimated contribution to the content of the manuscript lay between 45=50%. However, we also agreed that my contribution to the work as a whole was greater once I took up the responsibilities as senior author.

Abstract

Until recently, reports of footprints attributable to ankylosaurs have been historically rare. Prior to the late 1990's almost all discoveries were of small sites and isolated footprints with all but one site from rocks of Cretaceous age. One reason for the apparent rarity of ankylosaur track reports is that some of the footprints that we now regard as ankylosaurian were initially attributed to other quadrupedal dinosaurs such as ceratopsians or sauropods.

Tracksites recently discovered near Grande Cache in western Canada and the Cal Orcko site in Bolivia, significantly changed our previous perception of the abundance of ankylosaurid trackways, and even provided evidence of running behavior by one individual, and skin impressions in others. These sites also give some insight into the palaeoecology of ankylosaurs and indicates the variety of trackmakers that frequented the palaeoenvironments in which their tracks are found.

Probable ankylosaur tracks are now known from at least fourteen localities in North America, South America, Europe and Asia. Despite being poorly known, until very recently, possible ankylosaur tracks have been assigned to five ichnospecies, which in order of historical naming are: *Tetrapodosaurus borealis*, from the Lower Cretaceous of Canada, *Macropodosaurus gravis*, from the Lower Cretaceous of Central Asia, *Metatetrapous valdensis*, from the Lower Cretaceous of Germany, *Ligabuichnium bolivianum* from the Upper Cretaceous of Bolivia, and *Deltapodus brodericki* from the Middle Jurassic of England. We review these ichnotaxa and their probable affinities, as well as the basis for assigning certain quadruped footprints to the ankylosaurs.

Introduction

Despite the relative abundance of skeletal remains of ankylosaurid dinosaurs, their footprints, like those of other quadrupedal ornithischians (stegosaurids and ceratopsids)

are relatively uncommon (Thulborn, 1990; Lockley, 1991; Le Loeuff *et al.*, 1998). However, recent discoveries, especially in western Canada, where the first probable ankylosaurid footprints were recorded (Sternberg, 1932; Carpenter, 1984), and in Bolivia (McCrea, *et al.* 1998), have revealed a number of new tracks that we describe in more detail than those from other sites, owing to their much greater abundance. The purpose of this paper therefore is to briefly summarize all possible ankylosaur track reports and make preliminary morphological comparisons.

Based on the known geographical and stratigraphical distribution of thyreophoran dinosaurs (nodosaurids and ankylosaurids) we can predict a potentially widespread distribution of trackways in space and time (Carpenter, 1997a; 1997b; Carpenter and Kirkland, 1998; Coombs and Maryanska, 1990; Lockley and Matsukawa, 1998). To date however, with the possible exception of a single, Middle Jurassic site, all purported ankylosaur trackways are Cretaceous in age. The oldest purported thyreophoran prints have been found in the Lower Jurassic of Central France (Le Loeuff *et al.*, 1999). This evidence is supported by similar prints from the Liassic of Poland (Le Loeuff *et al.*, 1998; Lockley and Meyer, 1999; Gierlieski, 1999). We discuss these occurrences in relation to the sedimentary facies (where possible) in which the footprint assemblages occur.

CRITERIA FOR IDENTIFYING ANKYLOSAUR FOOTPRINTS

Given the value of the information that can be obtained from footprints, such as functional morphology, behavior and palaeoenvironment (Lockley, 1986; Farlow and Chapman, 1997) it is desirable to study footprints and attempt to identify the maker. Establishing the identity of any track maker can be a difficult undertaking (Farlow and Chapman, 1997) since many different animals may be able to produce very similar looking traces. Identification may be further complicated when these groups of animals

have overlapping geographic and stratigraphic ranges.

It is important to realize that the identification of footprints produced by ankylosaurs and the similarly sized ceratopsians have the potential to be easily confused, particularly those footprints which possess a pentadactyl manus and tetradactyl pes which are the most commonly found. Both of these groups are found in the Cretaceous and overlap in time (to some extent) and geography. Our intentions here are to rationalize preliminary criteria that will allow us to distinguish footprints produced by these two groups. A two pronged approach of morphological and biostratigraphic analysis is therefore necessary to discriminate between the tracks produced by ankylosaurs and ceratopsians.

I Morphological Analysis:

Skeletal Morphology: The morphology of the foot and hand skeleton should be considered, including the number and nature of the digits. A prediction of what types of footprints these animals might produce is possible using this type of evidence. Most taxa of ceratopsians (neoceratopsians) and ankylosaurs (ankylosaurids and nodosaurids) have five manual digits and four functional pedal digits. One exception (not the only one though) is *Euoplocephalus*, which only has three pes digits (Coombs and Maryanska, 1990).

Using *Sauropelta* to represent nodosaurid ankylosaurs (Figure 1a) and *Centrosaurus* to represent the neoceratopsians (Figure 1b) as contrasting examples, some differences in the manual and pedal skeleton are evident. It is important to note that we are only comparing relative proportions when referring to size, not absolute measurements.

The pes of *Sauropelta* is made up of four digits, with digit I being significantly shorter than digits II-IV (Figure 1a). The phalanges are relatively short as are the metatarsals. The unguals of the pes digits are bluntly pointed. The digits are relatively

wide and short. The foot skeleton is wider than it is long, but the animal could still produce a footprint that is longer than wide with the addition of a substantial metatarsal pad, which is quite likely to have existed as it does in some modern graviportal mammals. From skeletal material the natural position of the digits is difficult to know with precision. They would have been spread to different degrees in a living animal,

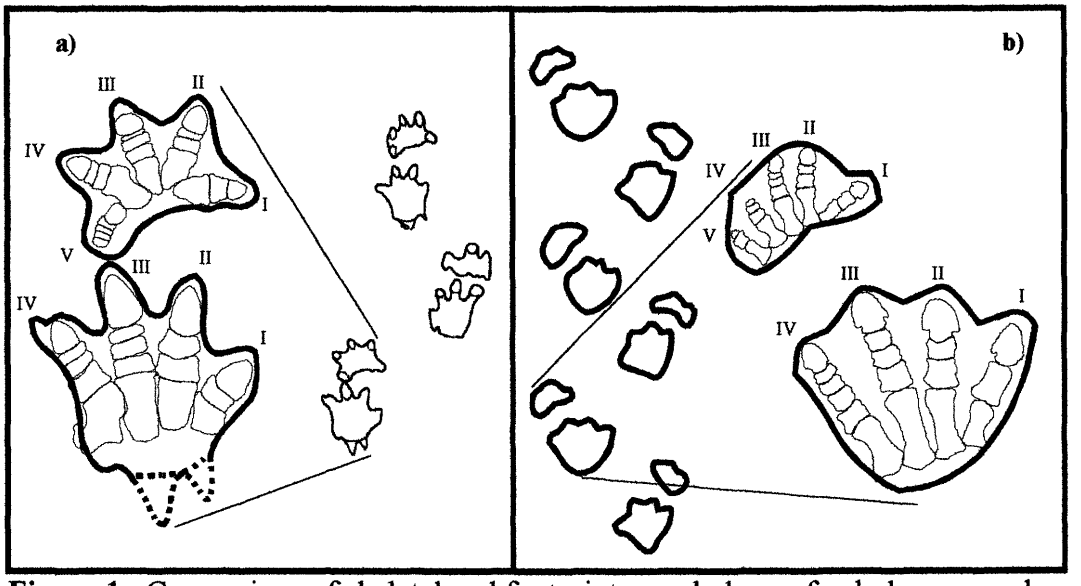


Figure 1. Comparison of skeletal and footprint morphology of ankylosaurs and ceratopsians. This illustration is to facilitate overall morphological comparisons between manus and pes skeletal morphology of ankylosaurs and ceratopsians (using *Sauropelta* and *Centrosaurus* respectively) and how these skeletal differences may appear in footprints (using *Tetrapodosaurus* for ankylosaurs and *Ceratopsipes* for ceratopsians). To this end the skeletal elements of *Sauropelta* and *Centrosaurus* have been adjusted in size for the comparative purposes, although relative dimensions and size relationships between the manus and pes remain intact. The footprints have been similarly adjusted.
a) *Tetrapodosaurus* prints (Sternberg, 1932) with skeletal elements of *Sauropelta* (modified from Carpenter, 1984) superimposed on the left manus and pes.
b)*Ceratopsipes* prints (Lockley and Hunt, 1994) with skeletal elements of *Centrosaurus* (manus and pes modified from Dodson and Currie, 1990) superimposed on the left manus and pes.

depending on its weight and gait, as well as the composition and consistency of the substrate.

The pes skeleton of *Centrosaurus* also has four digits (Figure 1b). Digit I is shorter than digits II-IV, but not as short in proportion to the other pes digits as digit I is

in *Sauropelta* (Figure 1a). The phalanges are relatively longer than those in *Sauropelta*, as are the metatarsals. The unguals are rounded and hoof-like. The foot appears to be nearly as long as it is wide (again this depends on several factors). The digits are relatively more slender and lengthier when compared to those of *Sauropelta*.

While there are some skeletal differences present, the pes footprint of these two genera would be very difficult to tell apart unless there were good indications of soft morphology differences (such as presence or absence of a fleshy pad that nearly envelopes the digits) or significant difference in the positioning of the digits. Many of the skeletal differences listed would be difficult to recognize in a footprint, especially if the footprint was poorly preserved or was produced in any but ideal substrates.

The manus of *Sauropelta* has five digits, digits II-IV being the longest, digit I being slightly shorter and digit V being the shortest (Figure 1a). All manual digits are composed of relatively short phalanges and carpels. The manus of *Sauropelta* is about two-thirds the size of the pes. Manual prints of this animal would display short, stubby digits with digit V being the most reduced. The unguals are subangular to rounded in shape.

The manus of *Centrosaurus* also has five digits with digit I being of intermediate length, digits II and III being the longest, and digits IV and V being significantly shorter (Figure 1b). The manual digits are composed of relatively short phalanges with a few being of medium (digit II) and long (digit I) length as well. The carpals of digits I-III are long, but those of digits IV and V are short. The unguals of digits I-III are rounded and hoof-like, but those of digits IV and V are smaller than the carpals that they articulate with. This gives digits IV and V the appearance of tapering distally. The manus is approximately one-half the size of the pes. Manus prints of this animal would show relatively long and slender digits I-III and reduced digits IV and V.

The skeletal differences between the manus of *Sauropelta* and *Centrosaurus* are more likely to be of use in identifying prints than those of the pes. Digit V in *Sauropelta*

is the only reduced manual digit, compared to the *Centrosaurus* manus where both digits IV and V are reduced. Also, the manual digits of *Centrosaurus* are longer and more slender in proportion to those in *Sauropelta*.

Footprint Morphology: First, it is the pes prints of both groups that are the most frequently preserved. Both ankylosaurs and ceratopsians (for the most part) have a tetradactyl pes, with the inner digit (I) the shortest. Based on a comparison of what we might consider the type material (*Tetrapodosaurus* and *Ceratopsipes* respectively), it appears that *Tetrapodosaurus* prints display longer toe impressions with less enclosing flesh (Figure 1a). This may be related to the fact that ankylosaurs generally have shorter metatarsals relative to toe length, whereas the ceratopsians have longer metatarsals relative to toe length, as described above. These ratios appear to have a morphogenetic origin (Lockley 1999 a, b and in press). In addition, *Tetrapodosaurus* pes prints have a shorter inner digit than *Ceratopsipes* which is also seen in the skeletal anatomy between *Sauropelta* and *Centrosaurus* (Figure 1a and b). This may be why ceratopsian (*Ceratopsipes*) pes prints appear more symmetrical that those of ankylosaurs (Figure 1a and b).

The orientation of the footprint may also be of some significance in making the ankylosaur-ceratopsian distinction. The middle digits, II and III of the pes, generally project forward, parallel to the parasagittal plane, in both *Tetrapodosaurus* and *Ceratopsipes*. However, the manus impression is located in front of the pes in *Tetrapodosaurus*, but in *Ceratopsipes* it is located slightly lateral.

Tetrapodosaurus manus prints are larger in proportion to the pes (about two-thirds the size of the pes), while *Ceratopsipes* manus prints are significantly smaller in proportion to the pes (about one-half the size of the pes). The size relationships between manus and pes prints are consistent with our comparison of *Sauropelta* and *Centrosaurus* manual and pedal skeletons. *Tetrapodosaurus* manus prints often have the

outer digits (I and V) arranged so that they are almost completely pointing backwards in relation to the direction of travel (Figure 1, 12 and 24b). In some specimens, digit I of the *Tetrapodosaurus* manus seems much more prominently displayed than the other manual digits (Figure 1a and 13). Manual digit I of *Ceratopsipes* does not seem quite as prominently displayed as that of *Tetrapodosaurus* (Figure 1b). Well-defined manus and pes prints from the Gething, Gates and Dunvegan Formations fit the ankylosaur pattern, as described above, very well.

To date only one purported ceratopsian ichnospecies has been named as *Ceratopsipes goldenensis* from the Maastrichtian of Colorado (Lockley and Hunt, 1995). In comparison with the anklyosaur prints described herein, *Ceratopsipes* has very blunt toes and is more transverse (wider than long) than forms like *Tetrapodosaurus*. The pes is also less symmetrical in ankylosaurian prints, with digit IV located much more anteriorly in relation to digit I than in *Ceratopsipes*, where the configuration of these digits is essentially symmetrical (Figure 1b).

The approach of comparing these two genera has the advantage that we are dealing with well preserved foot skeletons. A similar approach was used by Thulborn, (1990). However, one of the disadvantages is that we do not know how representative these genera are of the group as a whole. Clearly there is variation within both groups (ankylosaurs and ceratopsians) and we can predict that early, ancestral or primitive forms were smaller, with more slender toes than later, larger derived forms. To date no purported prints of small ancestral forms have been reported, so we have to compare footprints that belong to large species, whose lower level taxonomic affinities are unknown.

A new and very generalized approach has been suggested recently by Lockley (1999 a, b). First, it appears that the larger and more derived the track maker the more flesh it has on its feet. Though this is only a general rule it suggests that footprints may not always reflect the morphology of track maker's foot skeletons in detail, especially in

the case of larger animals. Although this does not help identify the track maker, it does point to the need to describe footprint morphology in its own right regardless of the track maker's identity. This point is often overlooked by non-ichnologists.

Pursuing this suggestion that footprint morphology must be examined in its own right, and in relation to other footprints (not only in relation to possible track makers), some general rules for footprint morphology have been empirically formulated. If we place all major dinosaur groups in a standard phylogenetic or cladistic arrangement (cf. Lockley 1999 a, figs, 4.5 and 7.5) we see a systematic (and size related) gradient in the relative width of the pes print in all clades, as well as a reiteration of this same gradient across the dinosaurian clade as a whole. In all cases the ancestral forms have narrower feet and the derived forms have wider feet. In addition, there is a tendency for more primitive forms to have less fleshy feet than derived clades, and for the step length to get shorter in derived clades.

Finally, it appears that flesh is first added to the rear of the foot in more primitive forms and progressively it creeps forward to enclose more and more of the distal extremities of the toes. Thus a sauropod has wider, fleshier feet with more enclosed toes, and a shorter step, than a theropod. The same goes for comparison between primitive and derived thyreophorans and cerapodans.

Any application of these principles to a comparison of ankylosaurian and cerapodan footprints must be considered tentative. However, one observation has been made that appears to be useful, and capable of being tested as more data becomes available. Ankylosaurian footprints of the *Tetrapodosaurus* type, reveal more slender and less enclosed digit impressions than ceratopsian footprints of the *Ceratopsipes* type. We must remember here that we have only this one named example of purported ceratopisd footprints with which to compare purported ankylosaur footprints.

If this preliminary integrated model of footprint and trackway morphology is valid, it predicts that there will be convergence between forms, such that the print of a

large highly derived ankylosaur would resemble a ceratopsian print more than a print of a smaller primitive species. Likewise, a small primitive ceratopsian might leave footprints that are convergent with those of ankylosaurs. Although generalized, this approach is both empirically derived and is based on the principle of comparative anatomy of footprints. Preliminary analysis suggests that in trackways of the same size, ankylosaurs will have slightly longer steps and slightly narrower, less fleshy feet (i.e., with more clearly separated digits) than ceratopsians (Figure 1a, b). We do not suggest that this is a model for the easy or fool proof differentiation of tracks of these two groups, only that it provides some generalized clues to comparative footprint morphology, that may be useful when considered in conjunction with other morphological and geological evidence.

II Biostratigraphic range of body fossils of potential track producers:

Neoceratopsians and ankylosaurs (nodosaurids and ankylosaurids) are large enough to produce the types of footprints we are surveying here. Traditionally it was assumed that ceratopsians and their tracks were confined to the upper part of the Late Cretaceous (Campanian and Maastrichtian), so that any large tetradactyl prints of the type described herein could not likely be considered ceratopsian in origin if they were pre-Campanian. This perspective has not significantly changed, as the earliest record of large ceratopsians are from deposits only dating back to the Turonian (Wolfe and Kirkland, 1998). Chinnery *et al.*, (1998) reported the occurrence of neoceratopsian teeth from the Lower Cretaceous Cedar Mountain Formation (Albian-Cenomanian boundary) and the Arundel Formation (late Aptian). As there are not yet any complete skeletons from these sites with which to indicate size or anatomy we still have to consider "large" neoceratopsians to be exclusively Upper Cretaceous, therefore it is unlikely that pre-Turonian "ankylosaur" tracks are of ceratopsian origin. Some of the most extensive and numerous tracksites are pre-Turonian, too early for the ceratopsians to be considered

responsible for producing them. On the other hand, the abundance and diversity of pre-Turonian ankylosaurs shows that they were present in the same time periods and geographic locations that many of our tracksites were formed, which strongly suggests that they may have been the trackmakers (Figure 2). Future discoveries of more complete, pre-Turonian neoceratopsians may cast our assertion into doubt. However, based on current evidence, there is a much stronger case for the ankylosaurs producing pre-Turonian footprints than there is for the ceratopsians.

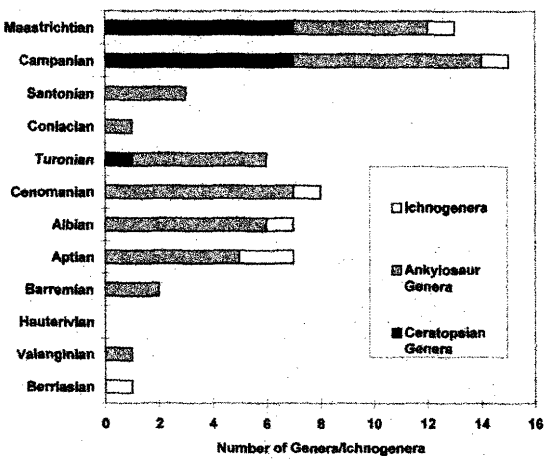


Figure 2. Cretaceous occurrences of ankylosaur (nodosaurid and ankylosaurid) and ceratopsian (excluding protoceratopsians and psittacosaurids) genera as well as purported ankylosaur and ceratopsian ichnogenera (Sternberg, 1932; Zhakharov and Khakimov, 1963; Haubold, 1971; Leonardi, 1984; Coombs and Maryaska, 1990; Dodson and Currie, 1990; Lockley and Hunt, 1995; Carpenter and Kirkland, 1998; Kirkland, 1998; Wolfe and Kirkland, 1998)

LIST OF SITES IN ASCENDING CHRONOSTRATIGRAPHIC ORDER:

Saltwick Formation, England (Aalenian-Bajocian)

Prints from the Saltwick Formation of Yorkshire, England, (Figure 3a) were named *Deltapodus brodericki* by Whyte and Romano (1994) who thought they were sauropod prints. Lockley *et al.*, (1994) expressed doubt, suggesting that these may be of thyreophoran origin because the pes prints appear too symmetrical to be of sauropodan origin and so are probably either an ankylosaur or a stegosaur. The lack of inward

rotation of the pes, and the bluntness of the digits is more reminiscent of ankylosaurs than other, stegosaur-like thyreophorans (Thulborn, 1990; Lockley, 1999a), but preservation is not good enough to allow fine discrimination of morphological detail. The conservative approach would be to label these as probable thyreophoran prints.

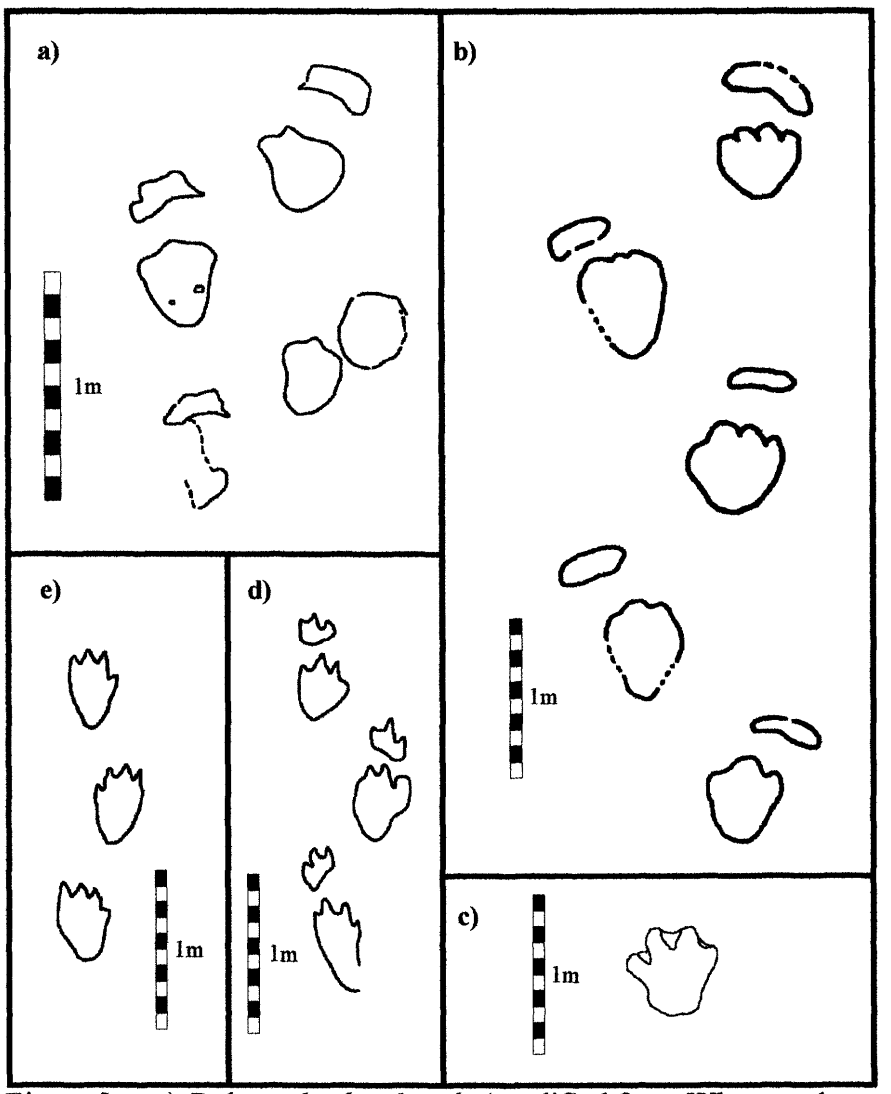


Figure 3. a) *Deltapodus brodericki* (modified from Whyte and Romano, 1994).
b) Purported ankylosaur track from the Purbeck Beds (after Ensom, 1988, Lockley 1991).
c) Isolated natural cast of possible ankylosaur pes from the Purbeck Beds (after Ensom, 1987)
d) *Metatetrapous valdensis* (Haubold, 1971)
e) *Macropodosaurus gravis* (Zakharov, 1964)

Whyte and Romano (1994) interpret the depositional environment the footprints are found in to be that of a, "..., marshy fluvio-deltaic environment with abundant evidence of lush vegetation"

Purbeck beds, England (Berriasian)

Footprints from the Purbeck beds of England (Figure 3b & c) have been interpreted as ankylosaurian in origin (Ensom, 1987, 1988; Lockley, 1991; Wright, 1996; Lockley and Meyer, 1999). These were also considered as possible sauropod prints and the beds were originally assigned to the Upper Jurassic (Ensom, 1987). Stratigraphic revisions now place these prints at the base of the Cretaceous (Berriasian) and most authors consider them as ankylosaurian (Wright, 1996, Lockley and Meyer, 1999). Ensom (1987) referred to the presence of skeletal elements of nodosaurid ankylosaurs from the Purbeck beds. While this does not prove the identity of the track maker as ankylosaurian, it does suggest that this assignment is very reasonable and probably correct. The footprints are found in a freshwater depositional environment which also contain the remains of freshwater fish, amphibians, turtles and crocodiles (Ensom, 1987, 1988).

Wealden Beds, Germany (Berriasian)

Metatetrapous valdensis (Haubold, 1971) from the Lower Cretaceous of Germany, is interpreted as ankylosaurian (Figure 3d). This ichnospecies is similar to *Tetrapodosaurus borealis* from Canada (discussed below) in having a tetradactyl pes with elongate heel and interior digit (I) shorter than the outer digit (IV). The manus appears to be tridactyl, but was probably pentadactyl with the inner and outer toes (I and V) not impressed.

The trackway originates from the Bueckeburg Formation, which is part of the Wealden Group, and consists of a series of siliciclastic sandstones with minor shales. The sequence is rich in boreal plant fossils, and also contains some freshwater bivalves and other invertebrate remains and traces. The depositional environment is considered to be that of a lowland fluvial coastal plain system. There is abundant evidence of shallow water in the form of both wave and current ripples (Mutterlose *et al.*, 1997).

Gething Formation, British Columbia (Aptian-Albian)

Sternberg (1932) described quadrupedal prints from the Lower Cretaceous (Aptian) Gething Formation of the Peace River valley, British Columbia, and named them *Tetrapodosaurus borealis* (Figure 4a and b). They were originally interpreted as being ceratopsian, but were subsequently identified as ankylosaurian in origin (Carpenter, 1984). We agree with this assignment, on the basis of both age and morphology of the prints. The type specimen was described from a series of fourteen footprints (seven manus, seven pes). A portion of this trackway (Figure 4a and b) is preserved as a plaster cast at the Royal Ontario Museum (NMC 8556). In the 1970s, expeditions to the Peace River canyon by the Provincial Museum of Alberta were unable to relocate the *Tetrapodosaurus* holotype. This single ankylosaur trackway was found among an ichnofauna dominated by *Amblydactylus* footprints which have been attributed to hadrosaurs (Currie and Sarjeant, 1979; Currie, 1983; Currie, 1995). The Gething Formation was part of a major deltaic complex and contains major coal deposits (Stott, 1972; Gibson, 1985).

Gates Formation, Grande Cache, Alberta (Lower Albian)

In recent years, several track sites have been excavated at the Smoky River Coal

Mine, near Grande Cache, Alberta (McCrea and Currie, 1998). Currently, sixteen ankylosaur tracksites are known from this coal mine, most of which occur on steeply dipping footwall slopes (McCrea and Currie, 1998). Most are similar to *Tetrapodosaurus borealis* (Sternberg, 1932) which, at present, is a monospecific ichnogenus. The sixteen sites are spread out over an area of approximately 25 km^2 and

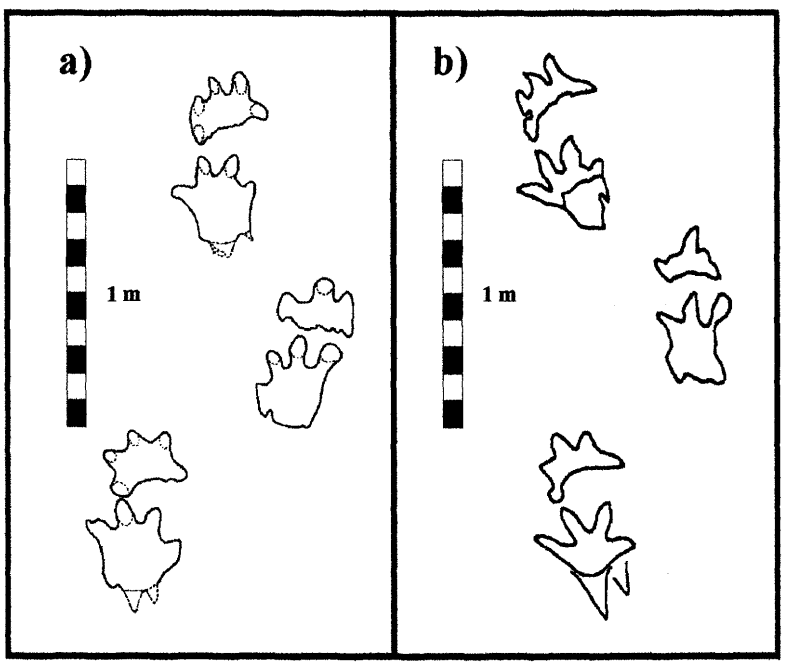


Figure 4. Two interpretative illustrations of the *Tetrapodosaurus borealis* holotype (NMC 8556) from the Peace River Canyon (Gething Formation).
a) *Tetrapodosaurus borealis*, NMC 8556 (Sternberg, 1932).
b)*Tetrapodosaurus borealis*, NMC 8556 (Currie, unpublished).

are treated as separate localities. The sites are labeled, using local mine designations: **E-2 Pit**, **W1a**, **W1b**, **W1c**, **W2**, **W3 Main**, **W3 Extension**, **W3 Corner**, **9 Mine**, **9 Mine West Extension (A and B)**, **9 Mine West Extension Fold Axis**, **Mine Dump**, **Center Limb Pit**, **8 Mine** and **12 Mine South A-Pit**. **E-2 Pit**, **W1a**, **W1b**, **W1c**, **W2**, **W3 Main**, **W3 Extension**, **and W3 Corner** are associated with a continuous outcrop along the limb of an anticline:

E-2 Pit: This tracksite was figured in Psihoyas and Knoebber (1994, p.189) and

shows several footprint sequences, some crossing over others (Figure 5). A few beds above this footprint layer is another footprint layer which shows several trackways navigating through a stand of fossil tree stumps with radiating roots (Figure 6). This site entered palaeontological folklore when a large part of the cliff collapsed (Psihoyas and Knoebber, 1994; McCrea and Currie, 1998). Psihoyas and Knoebber (1994, p.189) show before and after photographs revealing that most of the footprints at this spectacular site were destroyed. The rest of the footprints have subsequently been destroyed as a result of continued slope failure at this site.

Figure 5. *Tetrapodosaurus* trackways (photograph and illustration with stylized footprints) from E-2 Pit. White prints indicate underprints.
Photograph provided by Dr. Philip J. Currie.

W1a: A newly discovered site containing a dinoturbated area with a profusion of *Tetrapodosaurus* footprints (Figure 7).

W1b: A new site with several, short ankylosaur trackways showing good impressions of the feet and digits, preserved on friable substrate.

W1c: A small

site with a few *Tetrapodosaurus* footprints in one trackway.

W2: Another newly discovered, dinoturbated area with abundant *Tetrapodosaurus* footprints (Figure 8). There is evidence of gregarious behavior of two groups of animals displayed at this site. Each group traveled in a different direction, but the individuals, (three per group) within the respective groups were walking in the same direction. The spacing between individuals in each of the groups seems is consistent and the tracks do not cross, indicating that these animals were traveling together at the time the footprints were made. All of these preliminary observations were made from the ground. Further research is needed at this

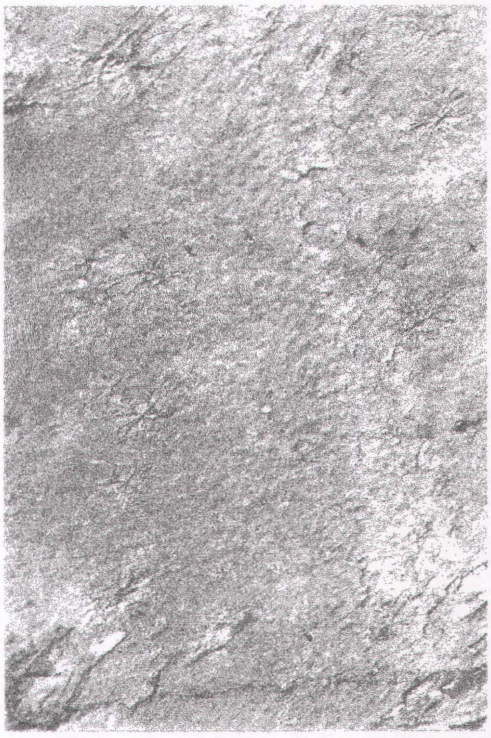


Figure 6. E-2 Pit site showing faint *Tetrapodosaurus* footprints associated with in situ tree stumps with radiating roots. Photograph provided by Dr. Philip J. Currie.

Figure 7. W1a site showing intense dinoturbation of *Tetrapodosaurus* footprints.

site.

W3 Main: The W3 Main footwall contains more than 6,000 footprints with over twenty *Tetrapodosaurus* trackways, some with more than 50 consecutive manus and pes prints (Figure 9 and 10). Some footprints preserved as natural moulds reveal skin impressions, making this a particularly significant site. Skin impressions were found on the posterior margin of a manus print that had been cast. The tubercles are elliptical measuring 7 mm x 2 mm. These skin impressions are on the edge of a mud bulge at the heel of the manus print and it appears that the tubercles were compressed anterior to posterior, but were probably originally rounded as those of other prints observed at this site and within the same footprint sequence.

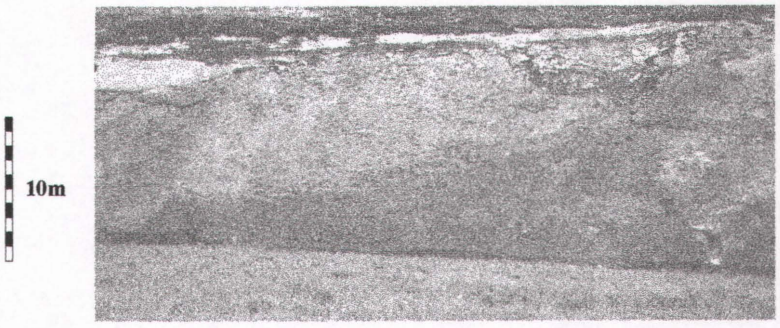


Figure 8. W2 site showing dinoturbation of *Tetrapodosaurus* footprints.

There are at least five layers of strata that contain variably preserved footprints at this site. Some footprints were made in substrate that had a relatively high water content, evidenced by the large mud bulges around the footprints (Figure 11). However, on the same bedding plane, just above the central prints in Figure 11, are footprints that appear to have been made after the substrate had

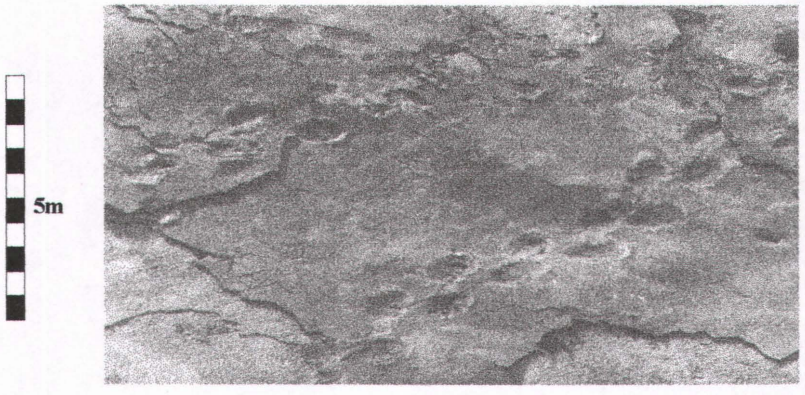


Figure 9. *Tetrapodosaurus* trackways at the W3 site associated with faint, tridactyl (*Ornithomimipus*) footprints.

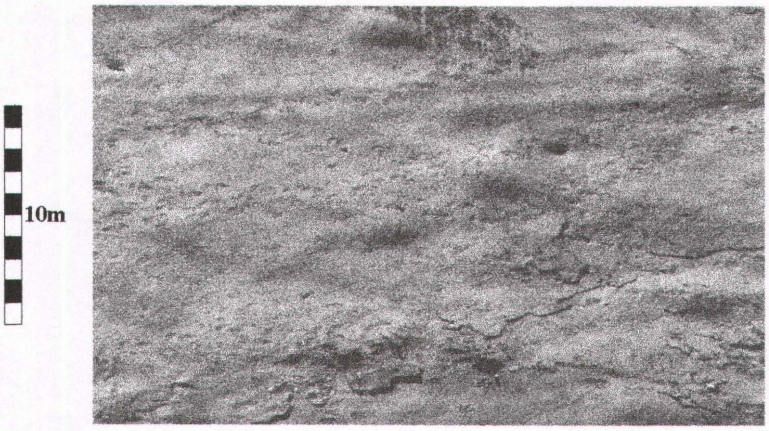


Figure 10. Lengthy *Tetrapodosaurus* trackways at the W3 site associated with equally lengthy *Irenesauripus* trackways.

dewatered somewhat. These prints are faint, but the digits are well-defined and do not display mud bulges. These prints are the same size as the other *Tetrapodosaurus* prints on this footwall. The pes prints show four elongate and slender digits with digits I and II being the most deeply impressed and with the tips of digits II to IV being very deeply impressed. The manus digits III to V are well-impressed, and digits I and II are present, though less deeply impressed (Figure 12).

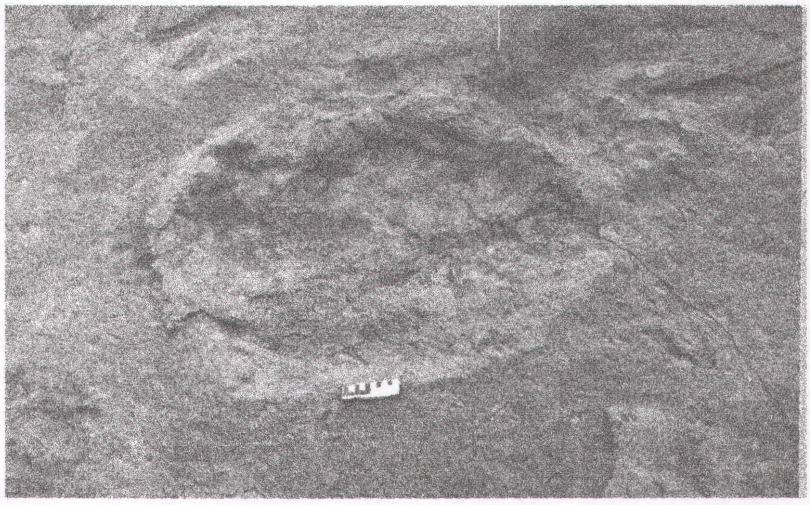


Figure 11. *Tetrapodosaurus* manus and pes (top center) with mud bulges at the W3 site (Scale is 10 cm).

There is a pair of parallel trackways that are proceeding in the same direction which could be interpreted as additional evidence of gregarious behavior of (adult) ankylosaurs based on footprints. The W3 Main ankylosaur footprints are associated with several other dinosaur (theropod) and bird ichnotaxa, making this among the most diverse ichnofaunas in the world (McCrea and Sarjeant, 1999).

Mine, near Grande Cache, Alberta (McCrea and Currie, 1998). Currently, sixteen ankylosaur tracksites are known from this coal mine, most of which occur on steeply dipping footwall slopes (McCrea and Currie, 1998). Most are similar to *Tetrapodosaurus borealis* (Sternberg, 1932) which, at present, is a monospecific ichnogenus. The sixteen sites are spread out over an area of approximately 25 km^2 and

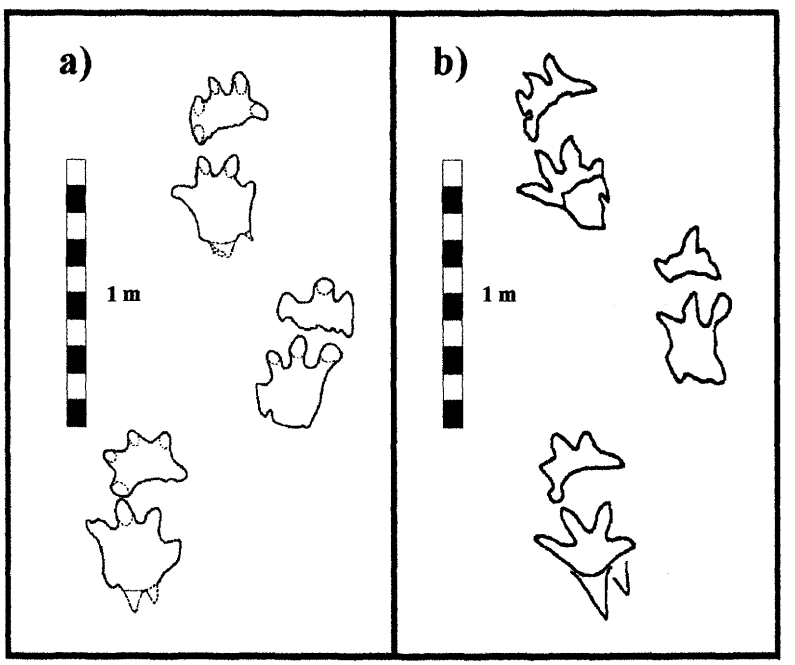


Figure 4. Two interpretative illustrations of the *Tetrapodosaurus borealis* holotype (NMC 8556) from the Peace River Canyon (Gething Formation).
a) *Tetrapodosaurus borealis*, NMC 8556 (Sternberg, 1932).
b)*Tetrapodosaurus borealis*, NMC 8556 (Currie, unpublished).

are treated as separate localities. The sites are labeled, using local mine designations: **E-2 Pit**, **W1a**, **W1b**, **W1c**, **W2**, **W3 Main**, **W3 Extension**, **W3 Corner**, **9 Mine**, **9 Mine West Extension (A and B)**, **9 Mine West Extension Fold Axis**, **Mine Dump**, **Center Limb Pit**, **8 Mine** and **12 Mine South A-Pit**. **E-2 Pit**, **W1a**, **W1b**, **W1c**, **W2**, **W3 Main**, **W3 Extension**, **and W3 Corner** are associated with a continuous outcrop along the limb of an anticline:

E-2 Pit: This tracksite was figured in Psihoyas and Knoebber (1994, p.189) and

W3 Extension: There are several *Tetrapodosaurus* trackways found high up on the footwall. A natural cast of a left manus print (Figure 13) that was recently collected from this site (TMP 99.49.2) shows well-defined digits (I-V), which fits our criteria for ankylosaurian prints.

W3 Corner: A few *Tetrapodosaurus* trackways are found very high up on the footwall.

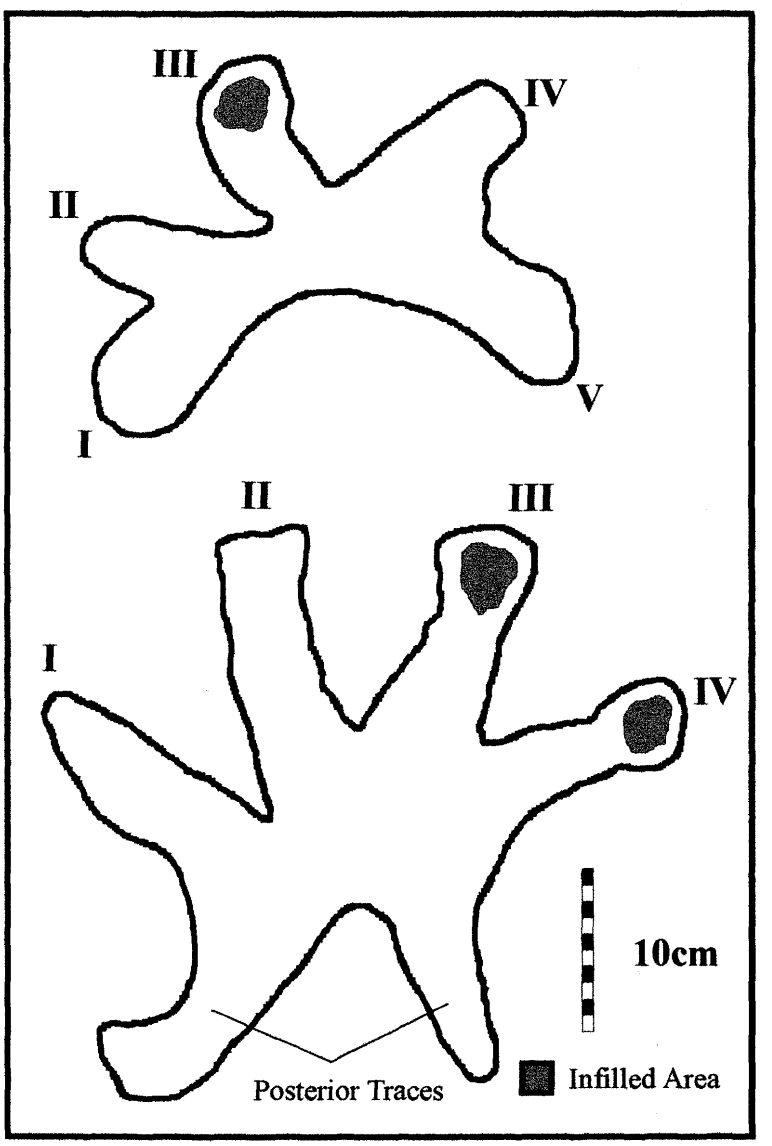


Figure 12. Outline of *Tetrapodosaurus* right manus and pes from the W3 Footwall, Grid B17/18, (McCrea and Sarjeant, 1999). A portion of these illustrated prints are seen in Figure 11, in the top right corner. Drawn from TMP 98.89.4 (replica cast).

12Mine South, A-Pit: Located on the anticline limb opposite the E-2 Pit-W3 Corner tracksites, this site boasts the longest *Tetrapodosaurus* trackways yet reported. The trackway consisted of over 120 consecutive manus and pes prints (McCrea and Currie, 1998) and was adjacent to another *Tetrapodosaurus* trackway of nearly the same length, but which proceeded in the opposite direction (Figure 14). One possible interpretation could be that this was the coming and going of one animal along a preferred route

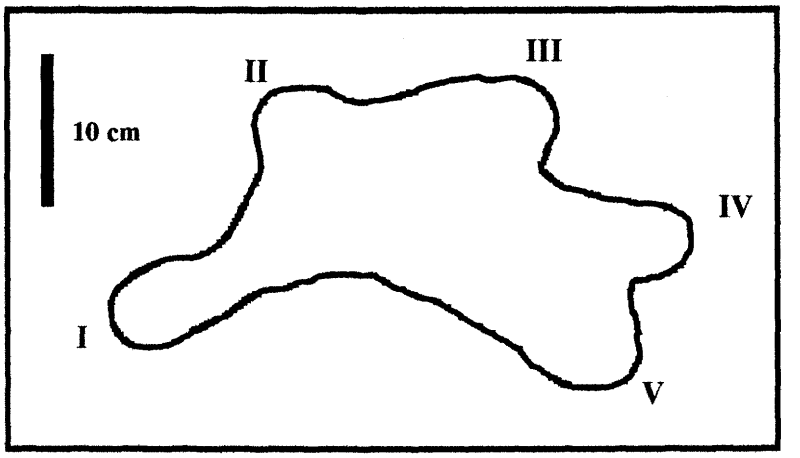


Figure 13. Illustration of a natural cast of a right manus print from the W3 Extension site (TMP 99.49.2).

(McCrea and Currie, 1998). There were several other *Tetrapodosaurus* trackways of lesser length at this site, but all were lost when the site collapsed over the course of the summer of 1998.

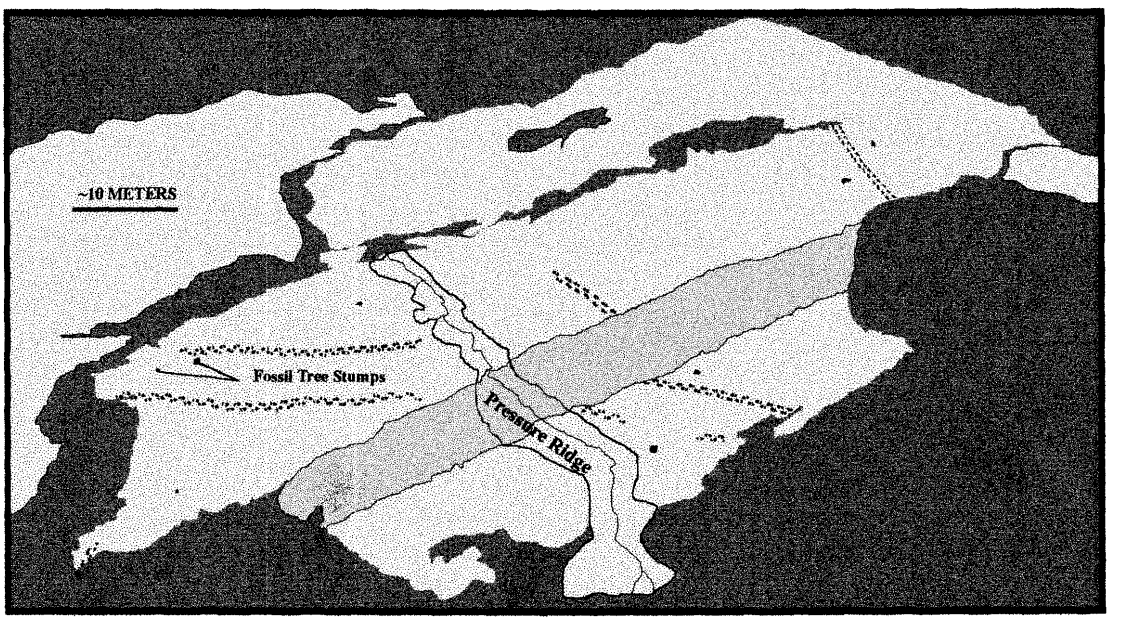


Figure 14. Illustration of the 12 Mine South, A-Pit, *Tetrapodosaurus* tracksite. Note: The formation of the pressure ridge figured herein split the two longest trackways almost in half.

9 Mine: A solitary ankylosaur trackway (Figure 15) was illustrated by Grady

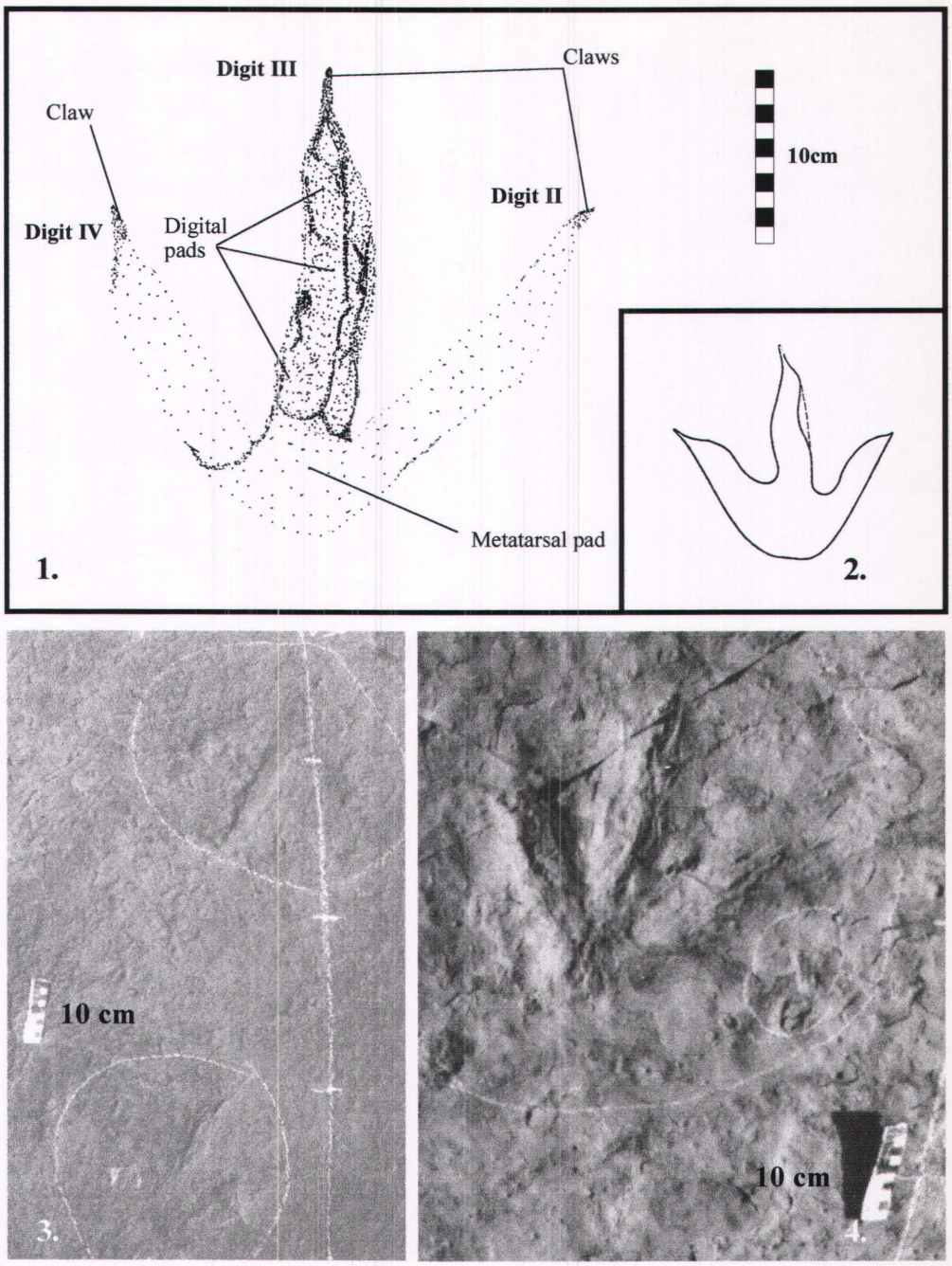


Figure 4.4.1-4: *Columbosauripus ungulatus* Sternberg 1932; 1, Left pes illustration of *C. ungulatus* drawn from a replica cast (TMP 98.89.6) from Grid K7. 2, Sternberg's (1932) illustration of *C. ungulatus* holotype (NMC 8551); same scale as Figure 4.4.1. 3, *C. ungulatus* footprint illustrated in figure 5.3 (Grid E23). 4, *C. ungulatus* footprints from figure 5.3 (B29).

average stride nears 160 cm. Step angle is generally under 120 degrees with the average being 110 degrees. Preliminary speed calculations based on Alexander's formula (1976) indicates that the animals who produced these footprints did so at a relatively unhurried walk (approximately 3km/h).

The Gates deposits were formed in a coastal plain or deltaic environment (Langenberg *et al.*, 1987) with abundant plant remains including ginkgoes, cycads, ferns, conifers and at least two species of angiosperms (Wan, 1996). *Tetrapodosaurus* prints dominate the Gates ichnofauna exposed in this region with footprints numbering in the thousands.

Shirabad Suite, Tadjikistan (Albian)

Footprints from Albian carbonates and evaporites of the Shirbad suite, discovered by F.H. Khakimov in 1963 (Zakharov and Khakimov, 1963) include the very distinctive track *Macropodosaurus gravis* (Zakharov, 1964), which we consider similar to *Metatetrapous valdensis* (Haubold, 1971).

The tracksite is situated in Shirkent National Park in the Hissar Range of Central Tadzhikistan. The footprints occur in Albian coastal carbonates and evaporites and comprise two trackways, including *Macropodosaurus gravis* (Zakharov, 1964). This trackway consists of alternating series of at least seven large tetradactyl prints. The prints are 50 cm long by 29 cm wide with a pace of 75 cm and a stride of 146 cm (see Figure 3e). These were previously attributed, incorrectly in our opinion, to a theropod (Zakharov, 1964).

Macropodosaurus gravis is very similar to the pes prints of *Metatetrapous valdensis* (Haubold, 1971) from the Lower Cretaceous of Germany. Similarities include pes size (length 50 cm and 44 cm respectively) and pes shape (pes longer than wide with a shorter digit impression on the inside). The pace angulation (about 145 degrees and

135 degrees respectively) is also very similar. The main difference between these two ichnotaxa is that *M. valdensis* is clearly the trackway of a quadruped with clear manus impressions as well as pes. The lack of manus prints in *M. gravis* however, could be due to overprinting, where the pes print overlaps the manus print partially or completely, which is common in large quadrupeds.

M. valdensis has been attributed to an ankylosaur (Haubold, 1971; Thulborn, 1990; Lockley and Meyer, 1999) and it is possible that *M. gravis* is probably also attributable to this group. Although this assignment is not proven, the Tadjikistan tracks are evidently not attributable to sauropods - thus it is reasonable to assign them to a large quadrupedal ornithischian. If *M. gravis* is indeed the same as or similar to *M. valdensis* at least at the ichnogenus level, the question arises as to whether the latter European material might not be considered a junior synonym of the material from Central Asia. Both ichnotaxa are in need of further detailed study if the type material can be relocated.

Cedar Mountain Formation, Utah (Albian - Cenomanian)

Footprints from the Mussentuchit member of the Cedar Mountain Formation (Kirkland *et al.*, 1997) of east central Utah, include two tetradactyl footprints of probable ankylosaurian affinity (Figure 17). These prints were discovered by Frank DeCourten (DeCourten, 1991) and first described by Lockley *et al.*, (1999). Their age is close to the Albian-Cenomanian boundary, and so are similar in age to footprints from the Dunvegan Formation. According to Kirkland *et al.*, (1997) the Mussentuchit member consists predominantly of drab gray, highly smectitic mudstone, that probably represents sedimentation that is almost continuous with the more carbonaceous overlying Dakota Group. The absence of calcareous nodules representing paleosols, is taken to indicate that this member represents a much wetter depositional environment

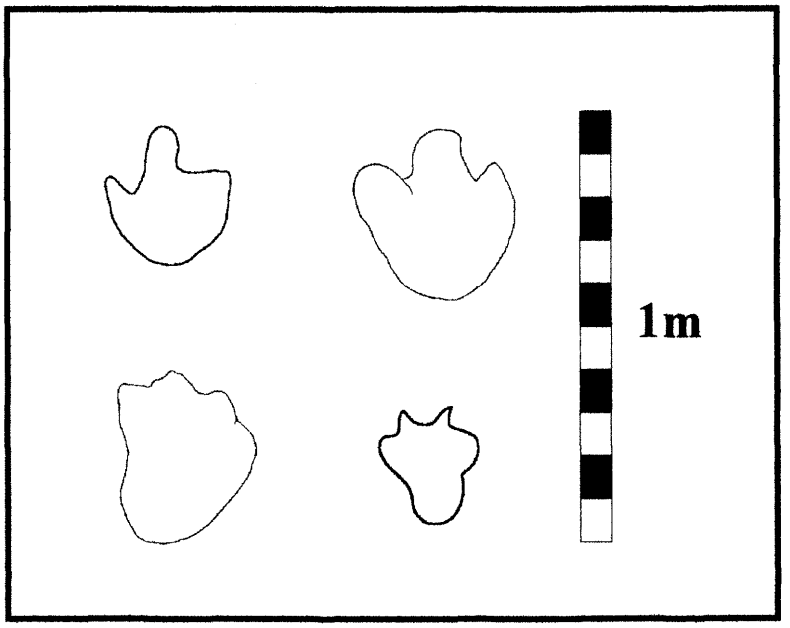


Figure 17. Cedar Mountain Formation prints, Utah (Albian-Cenomanian), after Lockley et al. 1997).

than the underlying members of the Cedar Mountain Formation, in part due to the transgression of the Mowry Sea (Kirkland, *et al.*, 1997). The fauna of this member includes small nodosaurid (cf. *Pawpawsaurus* [=*Texastes*]) and neoceratopsian teeth (Kirkland, 1996; Chinnery *et al.*, 1998). These are among the oldest neoceratopsian remains known, and suggest that it may be possible to find ceratopsian tracks as early as the mid-Cretaceous (Albian-Cenomanian Boundary). However the origin of ceratopsians is still poorly understood (Chinnery *et al.*, 1998) and it would be premature to speculate on the size or distribution of trackmakers. Below the Mussentuchit Member are the Ruby Ranch Member, the Poison Strip Sandstone and the Yellowcat Member which contain the skeletal remains of ankylosaurs including *Animantarx*, *Sauropelta* and *Gastonia*, respectively (Carpenter *et al.*, 1999). Notwithstanding the significant new discoveries of ceratopsians, it is still fair to state that ankylosaurs appear to have been more abundant and diverse at this time.

Dakota Group (Albian-Cenomanian)

Dinosaur tracks occur abundantly in the Dakota Group of Colorado and northeastern New Mexico. Until recently the only known types were attributed to ornithopods and gracile theropods (Lockley *et al.*, 1992). Recently however we have recorded a single four-toed print from a locality in Baca County Colorado. The specimen is about 27 cm long by 25 cm wide with one lateral digit (the one on the right - presumably digit I) shorter and more pointed than the other three (Figure 18). This print could be attributed to an ankylosaur, though, given the recent discoveries cited above, a neoceratopsian origin can not be ruled out.

Chandler Formation, Northslope, Alaska (Albian - Cenomanian)

Natural casts of tridactyl dinosaur footprints from the Chandler Formation near

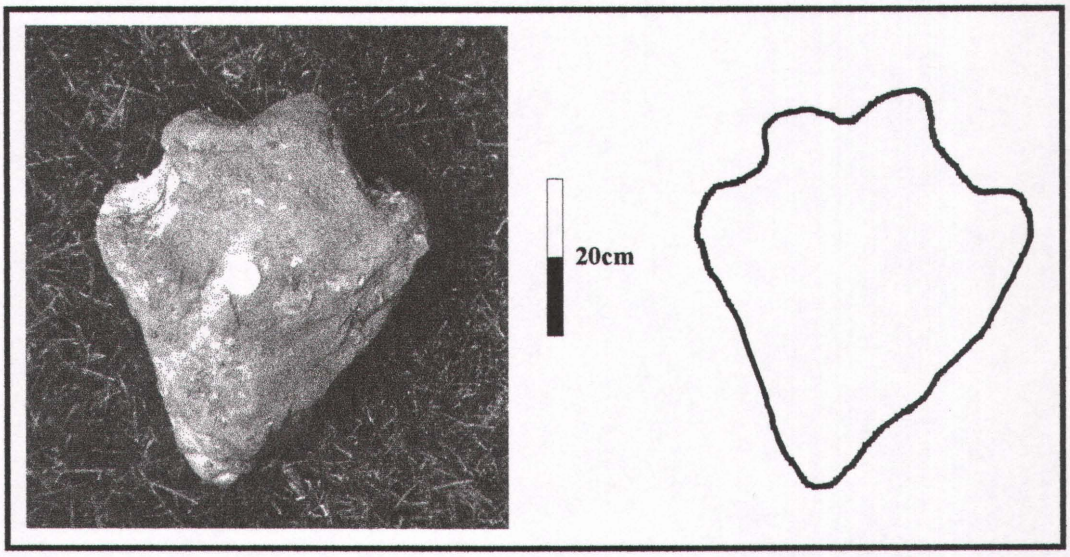


Figure 18. Probable ankylosaur pes print from the Dakota Group of Colorado (Baca County). Photograph and illustration.

the Colville River in Alaska have recently been reported and were tentatively identified as *Amblydactylus* (Gangloff, 1998). However, close examination of one of the footprints

revealed the presence of an additional, reduced digit (digit I), making this a tetradactyl footprint (Figure 19). Gangloff (pers. comm., 1999) reported additional collections in 1998 that have further substantiated the presence of tetradactyl footprints, and at least one natural cast of a partial manus print (KCM 98-5) with skin impressions (Figure 20). The tubercles on the manus print are round, measuring 4-6 mm diameter. These prints were very likely produced by ankylosaurs. The form of the natural cast figured in Gangloff, (1998, p. 217, figure 19 herein) is reminiscent of the natural casts of *Tetrapodosaurus* pes prints (Figure 16) of the Mine Dump near Grande Cache, Alberta (McCrea and Currie, 1998).

Footprints are nearly the only record of terrestrial vertebrates in the Chandler Formation and are found among coal-bearing deltaic sediments (Gangloff, 1998).

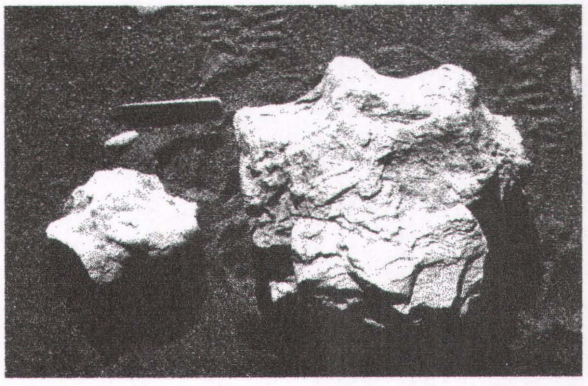


Figure 19. Probable ankylosaur pes print (right) from the Chandler Formation (Albian-Cenomanian) of Alaska. Pen in photograph is approximately 15 cm in length. Photograph provided by Dr. Roland Gangloff.

Figure 20. Probable ankylosaur manus print natural cast, KCM 98-5) with skin impressions from the Chandler Formation (Albian-Cenomanian) of Alaska. Photograph provided by Dr. Roland Gangloff.

Dunvegan Formation, Alberta and N.E. British Columbia (Cenomanian)

Currie (1989) reported the collection of a left manus print of *Tetrapodosaurus* (TMP 81.32.1) from the Murray River in northeastern British Columbia. Although Currie expressed uncertainty about the

stratigraphic position from which these prints originated, Dr. A. Guy Plint (written communication, 1997) has confirmed that similar prints are found throughout the Dunvegan Formation of northeastern British Columbia (Figure 21). This natural cast trackslab, found along the banks of the Pine River, includes a right and left tetradactyl pes and a right (incomplete) manus. The right pes is 37 cm wide and 40 cm long while the left pes is 37 cm wide and 39 cm long. The eroded remains of two manus prints are present in front of both pes prints, but they are in too poor of condition to get measurements from. This particular trackslab, has since been collected by a local resident with the use of rocksaws.

Additional ankylosaur prints are known from this area, some of which have skin impressions. One partial print, probably a pes, has skin impressions with round tubercles measuring 3-4 mm in diameter (Figure 22). A small pes print recently collected from a nearby creek bed (TMP 99.59.2) is significantly smaller than many other specimens mentioned herein and may be that of a juvenile ankylosaur (Figure 23).

A large sandstone slab with natural casts of a right manus and pes and a partial left pes from the Dunvegan Formation near Pouce Coupe, Alberta (TMP 94.183.1) is in

Figure 21. Natural casts of probable ankylosaur prints. Dunvegan Formation, N.E. British Columbia (Cenomanian). The right pes is at the bottom right, the partial right manus is at the top right and the left pes is at the top left. Scale is in cms. Photograph provided by Dr. A. Guy Plint.

collections at the Royal Tyrrell Museum of Palaeontology (Figure 24a). This specimen has the first recorded skin impressions from footprints of ankylosaurs (McCrea *et al.*, 1998). The tubercles are round, measuring 2-4 mm diameter on the pes and 1-2 mm on the manus. The right pes print appears tridactyl, but under oblique lighting a short, but well-defined digit I is visible with a small patch of skin impressions on it (Figure 24c). Digit I is also preserved on the partial left pes, but digits II-IV are absent, having been eroded away. The manus print (Figure 24b) has skin impressions as well, but also displays slide marks produced by tubercles on the posterior margin of the manus.

Figure 22. Probable print of an ankylosaur with skin impressions. Dunvegan Formation, N.E. British Columbia (Cenomanian). Photograph provided by Dr. A. Guy Plint.

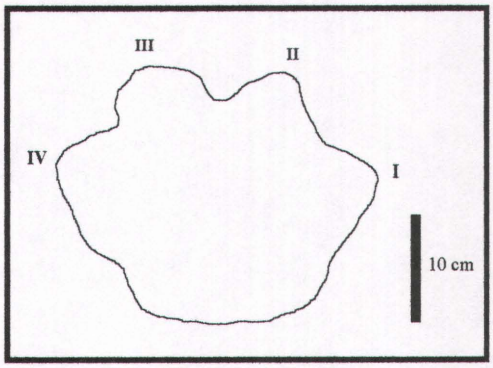


Figure 23. Illustration of a natural cast of a pes print (TMP 99.59.2) from the Dunvegan Formation, N.E. British Columbia (Cenomanian).

We feel that it is improbable that any of the Dunvegan prints could have been produced by a ceratopsian due to skeletal differences (particularly in the manus) and the fact that ceratopsians large enough to have made these prints are not yet known from this time.

Plint and Lumsden (written communication, 1999) observed that footprints found in the Dunvegan Formation are often preserved as natural casts on the base of tabular crevasse-splay sandstones, overlying dark gray mudstone of backswamp or

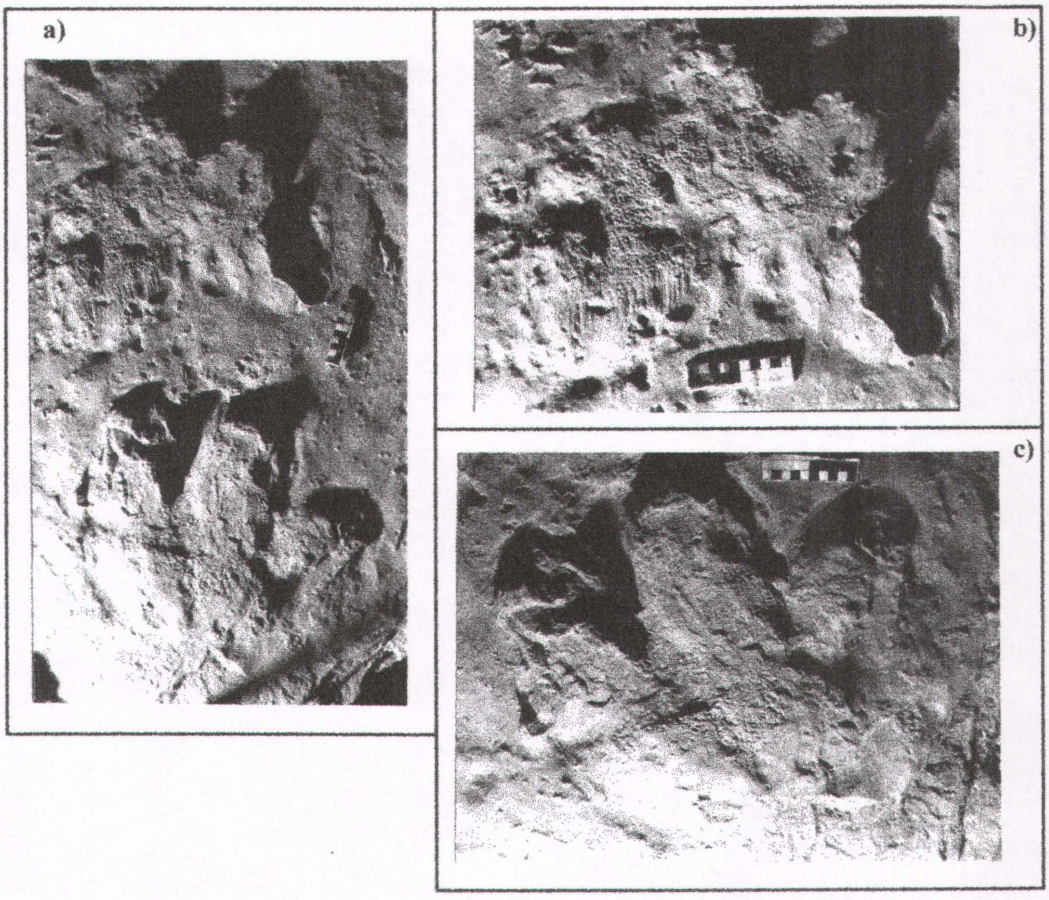


Figure 24. **a)** Natural cast of right manus and pes prints with skin impressions (RTMP 94.183.1). Dunvegan Formation, Western Alberta (Cenomanian). Scale is in cms.
b) Close-up of right manus from Figure 21a, showing slide marks produced by tubercles on the posterior margin of the print.
c) Close-up of right pes from Figure 21a, showing faint Digit I with patch of skin impressions.

lacustrine origin (see also McCarthy and Plint, 1998; Plint, 1996).

Blackhawk Formation, Utah (Campanian).

Several natural casts of tetradactyl prints previously identified as ceratopsian in the College of Eastern Utah Prehistoric Museum in the town of Price, Utah (CEUM 746, F-16 and 1834) are probably the pes prints of ankylosaurs (Figure 25). This identification is based on similarities to *Tetrapodosaurus* prints, asymmetry of the pes

and reduction of the presumed digit I. Other footprint specimens in the museum collections have been identified as ceratopsian based on the symmetry of the pes and their resemblance to *Ceratopsipes* prints. Carpenter (1992, Fig. 5) illustrated a tracing of a footprint from Parker and Rowley (1989, Fig. 40.23) with a *Styracosaurus* foot skeleton within it demonstrating the possibility that some of these prints were produced by ceratopsians.

The footprints are from coal mines near Price, Utah, where many footprints have been found in the past (Parker and Balsley, 1989; Parker and Rowley, 1989). Large tetradactyl prints of this age, like those from other upper Cretaceous sites described below, could have been made by ceratopsians, which were extant at the time. The sediments in which the footprints are found were formed in brackish and freshwater swamps as well as along lake-margins (Parker and Balsley, 1989).

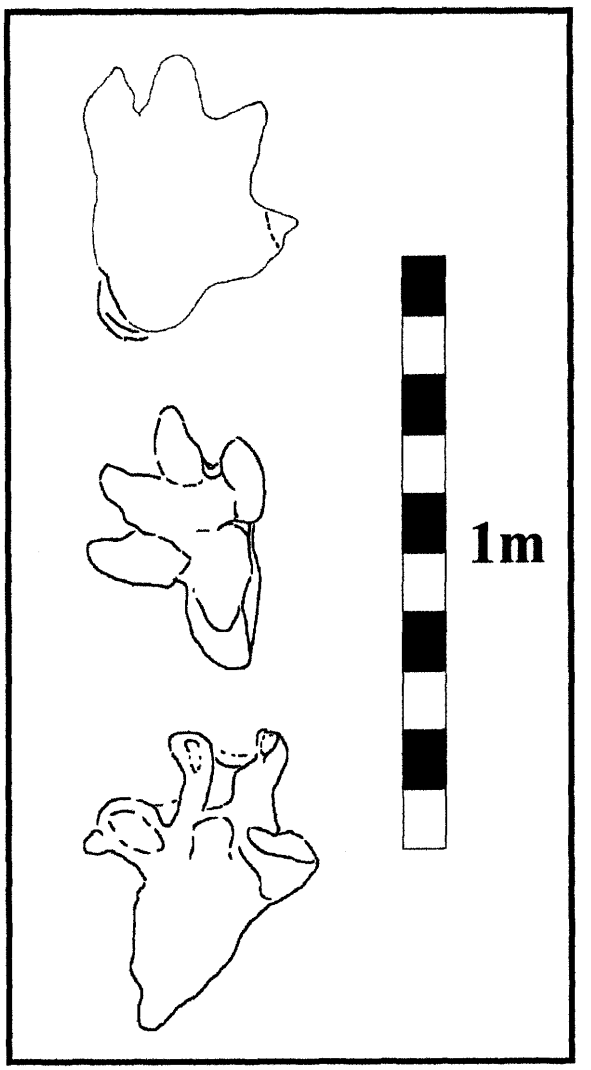


Figure 25. Tetradactyl footprints from the College of Eastern Utah Museum collection including footprints of both ankylosaurid and probable ceratopsid origin. Top: CEUM 746; Middle: F-16; Bottom: 1834.

Djadokhta Formation, Mongolia (Campanian)

Ishigaki (1999) recently reported the presence of "massive" quadrupedal footprints (digits 30-90 cm in length) from the Gobi Desert that could possibly be ankylosaurian. Ishigaki (1999) noted that

the footprints are found in a region known for its ankylosaur remains (Jerzykiewicz, 1997), but where large ceratopsians are absent. Ishigaki considers the pace angulation (80-90 degrees) to be that of wide-bodied track makers, such as ankylosaurids. The footprints are found in fluvial-derived sediments along with the fossilized remains of fresh water animals including molluscs, crocodiles, turtles and fish (Ishigaki, 1999).

Toro Toro Formation, Bolivia (Campanian)

Footprints described by Leonardi (1984) from the Upper Cretaceous (Campanian) Toro Toro Formation of the Potosi Group, Bolivia are possibly of ankylosaur origin. They were originally attributed to sauropods (Campbell, 1983), but subsequently were described in detail by Leonardi (1984) and named *Ligabuichnium bolivianum* (Figure 26). Leonardi (1984) indicated, that they were not well enough preserved to determine if they were ankylosaurid or ceratopsid. Subsequently, however, Leonardi (1994, p. 39) restated his position, inferring that the prints, "...may be attributed to an unusually large Ankylosauria." but went on to suggest that, "...if the footprint is interpreted as tetradactyl instead of pentadactyl, the trackway might have been made by a ceratopsian." The reasons for this statement are not altogether clear because, in most cases, both ankylosaurs and ceratopsians have a tetradactyl pes and a pentadactyl manus.

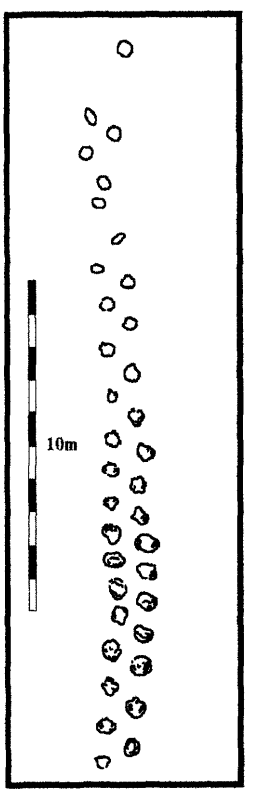


Figure 26. *Ligabuichnium bolivianum* trackway (Leonardi, 1984) from the Toro Toro Formation, Toro Toro site, Bolivia.

Cal Orcko site, El Molino Formation, Bolivia (?Maastrichtian)

Approximately a half dozen trackways of probable ankylosaurid origin have been found in the El Molino Formation at the Cal Orcko Limestone Quarry, near Sucre, in southern Bolivia (Figure 27 and 28). It is outside the scope of this review to describe these trackways in detail, as they are currently under investigation as part of a detailed study of this site. However, given the lack of convincing evidence for ceratopsians in South America (Huene, 1929: Weishampel, 1990), and the resemblance of the Bolivian footprints to other ankylosaurian prints described herein, suggests that they may be ankylosaurian. Further work is necessary to determine whether the prints from Cal Orcko should be attributed to the ichnogenus *Ligabuichnium*, *Tetrapodosaurus* or some other ichnotaxon.

As shown in Figure 27 there are several long trackway segments known from the Cal Orko site. One (T/3/4/2) appears, at first sight, to be that of a bipedal animal (Figure 27 and 28). The trackway reveals a long step and stride (1.5-1.65 m and 3.0 to 3.3 m respectively) which evidently indicates an individual running or moving at a fast trot of between 11 and 12 km per hour, based on the formula of Alexander (1976). Tracings were made of all the footprints to produce the composite shown in Figure 27, (T/2/3/8) which shows an ankylosaurian footprint morphology comparable to many of the examples cited above.

Trackway T/3/5/2 is characterized by footprints in which the rear margin is angled in an anterio-medial to postero-lateral direction, especially on the right side of the trackway. Toe impressions however point anteriorly. Footprints on the left side tend to have inwardly rotated toe impressions and less transverse posterior margins.

Trackways T/4/5/1 and T/4/5/4, which occur in the same layer as T/3/5/2, are remarkably transverse with transverse posterior margins. This mode of preservation

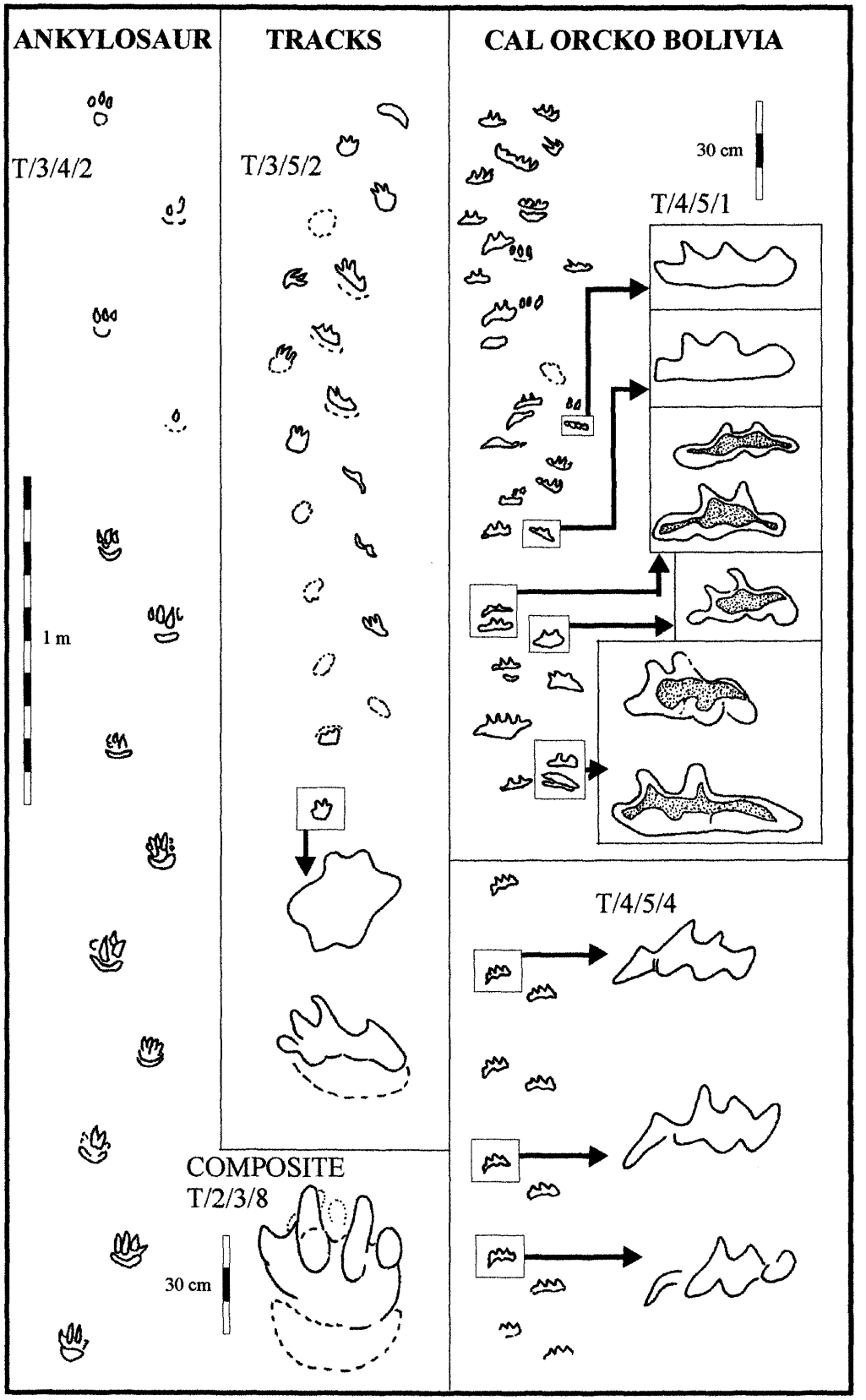


Figure 27. Ankylosaur trackways from the El Molino Formation, Cal Orko Site, Bolivia.

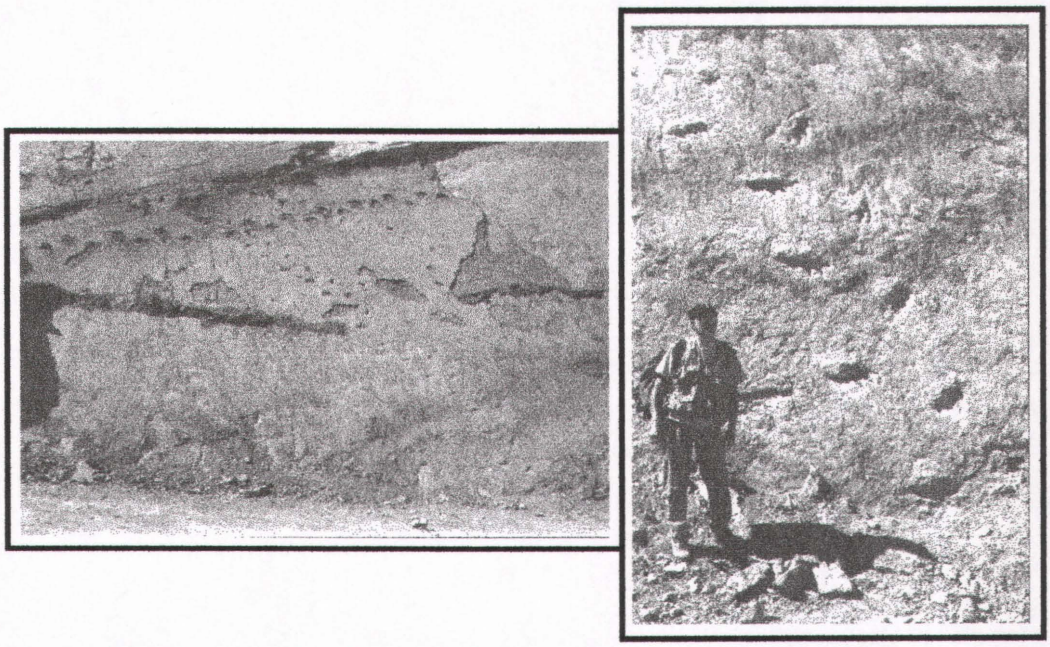


Figure 28. Photographs of an ankylosaur trackway from the El Molino Formation, Cal Orko Site, Bolivia (T/3/4/2). The horizontal trackway across the top of left photograph has been attributed to a sauropod. Dr. Giuseppe Leonardi is standing next to the ankylosaur trackway (T/3/4/2) in the right photograph.

seems to suggest that the prints were perhaps made on an overlying layer of sediment, and represent the penetration of the distal portion of the toes into an underlayer. The short stride indicates that these animals were not running. Many manus impressions are overprinted, but where pes sets are visible, both show that the central toes (digits II and III of the pes and also ?II and ?III of the manus) are the longest and most prominent.

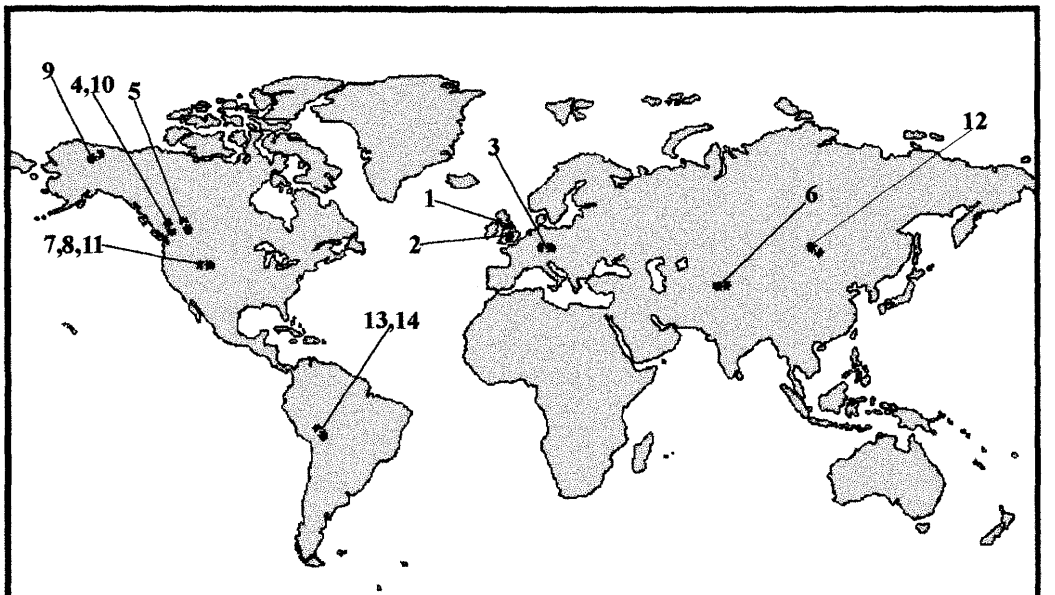
These footprints are found around the margins of ephemeral and perennial lakes; based on episodic pedogenesis and lacustrine stromatolites. The ankylosaur tracks occur in two levels that also yield remains of fresh water organisms such as catfish, turtles, crocodiles as well as snails, and charophytes (Meyer *et al.*, 1999 and in press).

GENERAL DISCUSSION

To date, there are fourteen probable ankylosaur tracksites known worldwide

(Figure 29). It is notable that, although few sites have been studied in detail, there are already five ichnospecies names assigned, all in different ichnogenera. It is outside the scope of this paper to enter into detailed systematic discussion. However, the first step, to record occurrence and briefly describe and illustrate the material is at least accomplished herein. It remains to be seen to what extent tracks from all fourteen sites are comparable in detail, and whether 1) the morphological features warrant interpretations of all tracks as ankylosaurian, and 2) whether the morphological features of various ichnites are sufficiently distinctive to warrant assignment of different ichnogenera.

At present there is no obvious pattern discernible in the geographical distribution of ankylosaur tracksites, although there is a temporal clustering of sites in the Albian-



14. El Molino Formation, Cal Orcko site, Bolivia (?Maastrichtian)
13. Toro Toro Formation, Bolivia (Campanian): type locality for *Ligabuichnium bolivianum* (Leonardi, 1984)
12. Djadokhta Formation, Mongolia (Campanian).
11. Blackhawk Formation, Utah (Campanian).
10. Dunvegan Formation, Alberta and N.E. British Columbia (Cenomanian).
9. Chandler Formation, Northslope, Alaska (Albian - Cenomanian).
8. Dakota Group, Colorado and New Mexico (Albian-Cenomanian)
7. Cedar Mountain Formation, Utah (Albian - Cenomanian).
6. Shirabad Suite, Tadjikistan (Albian): type locality for *Macropodosaurus gravis* (Zakharov, 1964).
5. Gates Formation, Grande Cache, Alberta (Lower Albian).
4. Gething Formation, British Columbia (Aptian-Albian): type locality for *Tetrapodosaurus borealis* (Sternberg, 1932).
3. Wealden Beds, Germany (Berriasian): type locality for *Metatetrapous valdensis* (Haubold, 1971).
2. Purbeck Beds, England (Berriasian).
1. Saltwick Formation, England (Aalenian - Bajocian): type locality for *Deltapodus brodericki* (Whyte and Romano, 1994).

Figure 29. Location and list of purported ankylosaur tracksites.

Cenomanian. It is also apparent that almost all known sites are Cretaceous in age. As indicated above, it is not certain if the Jurassic tracks from England are ankylosaurian in origin (Lockley *et al.*, 1994). The Gething, Gates and Dunvegan Formations are within two of the three Cretaceous cyclic, clastic sequences found in western Alberta and northwestern British Columbia (Stott, 1975; 1982; 1984). This sequence shows evidence the continuous presence of ankylosaurs evidenced by footprints during the early part of the Cretaceous in this part of the world. The high concentration of Aptian-Cenomanian sites (50%) in western North America could be considered a real paleogeographical phenomenon indicating a higher concentration of track makers in this region, but it might also be an artifact of preservation.

Current biostratigraphical constraints would seem to suggest that it is unlikely to find ceratopsians in pre-Cenomanian or pre-late Albian deposits. Such inferences seem to rule out the possibility that any of the older ichnofaunas (1-10, Figure 29) could perhaps be ceratopsian rather than ankylosaurian as we infer. The large size of many of the later Albian and Cenomanian tracks described herein, and the fact that ankylosaurs were particularly abundant at this time, also makes it unlikely that any of the footprints might be those of early ceratopsians that had already attained large body sizes. The possibility that some South American footprints might be ceratopsian in origin has already been discussed and is largely ruled out by paleobiogeographical considerations. In fact, to date, it is only in the Blackhawk Formation assemblage that we find a collection of isolated, and somewhat out of context footprints that might be of both ankylosaurian and ceratopsian origin.

Another valuable byproduct of the increase in discovery of ankylosaur footprints has been the recognition of prints with skin impressions, found in the Albian-Cenomanian (Gates, Chandler and Dunvegan formations). It is outside the scope of this paper to fully describe this material, but the tubercles all appear to be round, though of varying diameter. This moderately well-preserved material will allow us to compare

skin surface textures of ankylosaurs with those of contemporary or near contemporary ornithopods (Currie *et al.*, 1991) as well as non-contemporary large herbivorous dinosaurs such as sauropods (Czerkas, 1992; 1994). It is also theoretically possible that the study of these tracks will ultimately help distinguish them from ceratopsian footprints, though to date no ceratopsian footprint skin impressions have been described.

ANKYLOSAUR PALEOENVIRONMENTS AND PALEOECOLOGY

There has been some discussion about the habitat preference of ankylosaurs. Carpenter (1997b) observes that ankylosaur distribution was dependent on the distribution of the plants which made up their diet. He also noted that North American ankylosaurs were found in moist coastal areas, while Asian ankylosaurs tend to be found in arid to semi-arid environments. The track record of ankylosaurs clearly has a significant bearing on this discussion, and shows that they did not shy away from moist environments. In fact, ankylosaurs, with footprints numbering in the thousands, dominate the Smoky River ichnofauna of the Gates Formation (McCrea and Currie, 1998), which is a coastal plain depositional environment that had once supported large coal swamps (Langenberg *et al.*, 1987).

Ankylosaur footprints are concentrated in coal-bearing and floodplain facies (Blackhawk, Cedar Mountain, ?Chandler, Dunvegan, Gates, Gething, ?Saltwick and Wealden formations), that seems to suggest a strong facies preference for well-vegetated, well watered lowlands. The Purbeck, Toro Toro and Cal Orcko settings were not necessarily very different in terms of food and water supplies available to large dinosaurs. The El Molino Formation in Bolivia provides evidence that ankylosaurs lived around fresh water depositional settings.

It is evident that ankylosaur tracks are no longer nearly as rare as once thought (Lockley, 1991; Schult and Farlow, 1992). It has been noted that tracks of large

ornithischians (stegosaurs, ankylosaurs and ceratopsians) are rarer than might be predicted on the basis of relatively abundant skeletal remains. It has been suggested that perhaps this was due to the preference of these animals for dry (e.g., upland or inland) habitats where tracks would not be preserved rather than humid (or lowland/coastal) settings (e.g., Lockley and Conrad, 1987). While this may be true in the case of stegosaurs (Buffrenil *et al.*, 1986; Dodson *et al.*, 1980; Galton, 1990), it appears that this generalization does not extend to ankylosaurs or ceratopsians. For example, ceratopsian footprints are best known from coastal plain facies where they were made on very wet substrates (Lockley and Hunt, 1995). Retallack (1997) goes so far as to refer to "soggy ceratopsians" and indicate that, "...some ceratopsians such as *Styracosaurus* lived in swamps." It now appears that ankylosaur tracks are associated with low-lying flood plain and coastal-plain facies assemblages, and so can not be considered solely dry land or upland animals on the basis of ichnological evidence.

Looking at the palaeoenvironmental setting of a few ankylosaur skeletal sites we see that palaeoenvironmental interpretations derived from tracksites (preference for low-lying wetlands) are generally supported. The depositional environment of the Arundel Formation has been compared to the Mississippi delta with oxbow swamps (Kranz, 1998; Lipka, 1998) and contains the remains of nodosaurid ankylosaurs. The Cloverly Formation, where the skeletal remains of *Sauropelta* are found, also contain the remains of aquatic animals like fish (*Amia* and lungfish) as well as crocodiles and turtles (Ostrom, 1970) indicating that *Sauropelta* frequented the margins of freshwater environments. The Judith River Formation of Alberta contains the fossil remains of ankylosaurs (Brinkman, 1990) as well as a variety of terrestrial and aquatic taxa (Brinkman, 1990, Table 1). Eberth (1990) describes the Judith River Formation as a, "...channel-facies dominated, coastal plain sequence,...". Significant numbers of ankylosaurs have also been found in marine deposits suggesting that they were washed out to sea (Eaton, 1960; Horner, 1979; Lee, 1996). Such taphonomic contexts suggest

that the animals may have been transported by rivers or floods into the marine environment, and that they had presumably lived in coastal areas. We note however that the ankylosaur (*Pinacosaurus*) from the Campanian age Djadokhta Formation of Mongolia is found "...in semi-arid, alluvial-to-eolian settings", but some dune beds may have been, ",...organically rich and seasonally moist" (Jerzykiewicz, 1997, p. 188). The recent report of probable ankylosaur footprints from fluvial-derived substrates in Mongolia (Ishigaki, 1999) suggests that some Mongolian ankylosaurs lived on the margins of freshwater environments.

Given the increase in ankylosaur tracksite reports from two in 1991 (Lockley, 1991) to fourteen (herein), it is clear that previous perceptions of scarcity were an artifact of limited data rather than scarcity in the track record. With the abundance of footprints reported at certain sites, such as the Smoky River ichnofauna (Grande Cache), we can ask if there is a possibility that trackways might point to gregarious behavior among ankylosaurs. Trackways and inferred ankylosaurian dinoturbation are sufficiently abundant at Grand Cache sites W3, 12 Mine South, A-Pit, W1a and W2 to raise this question. *Pinacosaurus* skeletons from Djadokhta Formation (Jerzykiewicz, 1997) also indicate a social group or clutch of juveniles that died together and were buried by a sandstorm. Like other large herbivorous dinosaurs, some ankylosaur taxa were probably gregarious. Further study is required to determine the extent to which this can be demonstrated using ichnological data.

It is outside the scope of this summary to provide detailed discussion of the ichnotaxa associated with the ankylosaur track assemblages outlined herein. However some general observations are pertinent. It appears that only in the examples from the Purbeck, Wealden, Toro Toro and Cal Orko sites is there evidence of sauropods in association with ankylosaur footprints. This may reflect the sauropod preference for carbonate substrates rather than an association between these two groups (Lockley *et. al.*, 1994). Theropod footprints also occur at these localities, and at the two European

sites we also find ornithopod (iguanodontid) prints. At the North American sites quite rich, though as yet little described ichnofaunas are present, including ornithopod prints, theropod prints and, at all the Canadian sites, bird footprints. At most sites sauropod footprints are conspicuous by their absence owing in large part to the late Albian-Maastrichtian sauropod hiatus in North America (Lucas and Hunt, 1989).

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